

Pterosaurs – flying time machines

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I am going to talk to you about a group of animals that are really quite fascinating for all sorts of reasons but mainly because they can fly. We have a lot to learn from pterosaurs because they are so beautifully engineered and in this talk I am going to examine aspects of their anatomy and discuss their diversity and history.

Now of course we can fly (in aeroplanes); but this is expensive in terms of the energy required to do it. Flight has evolved several times in the animal kingdom but man has had to do it through cultural means and the use of technology. Flight (powered flight, not gliding) first evolved in the Carboniferous invertebrate world of the insects. No other invertebrate group has evolved active powered flight. How did they do it? Well we know that they grew wings but they had to evolve wings from something; perhaps they evolved from lateral appendages such as gills. Larval ephemeroptera have gill structures which are superficially wing-like but they are lateral membranes with veination and functions as gills, but it can be imagined that if they thickened and lengthened they would come to resemble wings.

We are all familiar with birds who fly very beautifully and gracefully; there are all sorts of controversies about how birds gained the power of flight. It is relatively easy to examine and understand the anatomy of the bird skeleton and we can work out what skeletal modifications had to take place in order to develop their wing. From this and from good fossil evidence, it would appear that birds are derived from small theropod dinosaurs. Many small theropod specimens have been found in China that have structures in the integument that may be interpreted as proto-feathers, feather-like structures or even true feathers. Controversies arise over why feathers evolved in the first place. Did feathers evolve simply for flight? The answer is almost certainly "No". Did they have some other purpose? The answer is almost certainly "Yes". Could it be for insulation? That would allow dinosaurs to have evolved small bodies; if they could insulate themselves they could have small bodies without losing heat and that would have allowed them to become nocturnal. Perhaps they evolved feathers for sexual display and they became secondarily co-opted for flight. The late Jurassic *Archaeopteryx* from Solnhofen, Germany, shows beautiful impressions of feathers on an ordinary dinosaurian-type hand and a dinosaurian-like tail, clad in feathers. There have to be some ancestors to this animal that also possessed feathers, perhaps somewhere in the Lower Jurassic, although none has yet been found.

Bats are another group of vertebrates that achieved active powered flight; with a record going back into the Eocene. Thus bats have been flying for around about 55Ma while birds have been flying for probably 145Ma and quite likely a bit longer. Insects, on the other hand, have probably been flying for nearly 400Ma. Insects, bats and birds are still with us and still flying but pterosaurs, flying reptiles of the Mesozoic, were first on the scene towards the end of the Triassic but became extinct at the end of the Cretaceous. They seemingly appeared from nowhere about 220Ma ago: the first pterosaurs in the fossil record are fully developed flying animals; there are no intermediate animals between a ground-dwelling four-legged animal and the flying

pterosaur. There are a few animals that have been suggested as possible ancestors but analysis of their skeletal structure has generally ruled them out; so we do not know from which group they evolved. At the end of the Cretaceous they disappear very suddenly, and at the same time that the large dinosaurs disappeared. So they too had a pretty good innings in the sky and it is rather sad that they did not leave any descendants. Similarly there is no animal alive today that we can recognise as being descended from an animal that was the putative ancestor of pterosaurs. So, in terms of their relationships to other animals, there are still many unanswered questions and we are only able to examine their flight by analysis of their meagre fossil record.

A study of their anatomy is made all the more difficult as they have undergone so many skeletal modifications for flight that trying to work out from which group of animals they derived has always been problematic. Indeed, in the early days, when pterosaurs were first discovered, they were put into all sorts of groups and it took quite a long time before they were recognised as flying animals. Despite the fact that Cuvier had determined that pterosaurs had been flying animals and were reptiles, a reconstruction in the 1830s depicted pterosaurs as aquatic and supposed that their elongate fourth finger was enclosed in a large paddle as in some turtles; quite clearly this reconstruction failed to consider the stresses that would be applied on these joints at the distal end of a paddle when rowing through the water. One stroke and it would have broken the finger in several places. Yet another reconstruction depicted pterosaurs as a type of marsupial bat; however, it was based on evidence that pterosaurs possessed fur which has since been supported by more recent discoveries. The presence of fur is supported by recent discoveries, but clearly they were not marsupials.

The anatomy of pterosaurs is rather bizarre. There are broadly two types of pterosaur; long tailed forms and short tailed forms, the so-called rhamphorhynchoids and pterodactiloids respectively. Pterosaurs look head heavy with massive skulls compared with their relatively tiny bodies (Figure 1). The body is usually considerably shorter than the skull and those forms with large

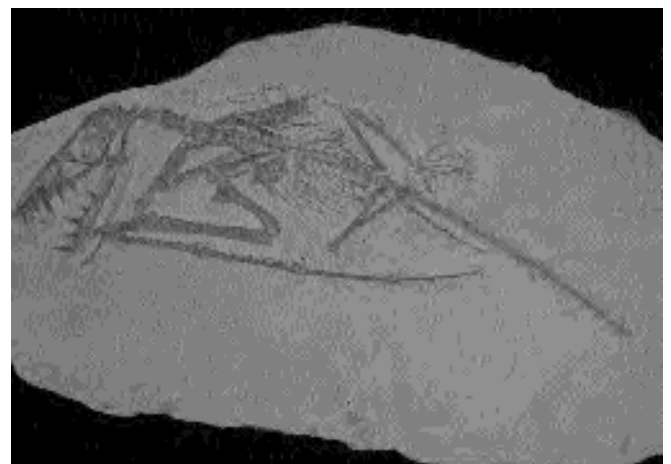


Figure 1. *Scaphognathus crassirostris*, a long-tailed pterosaur. Photo Dino Frey.

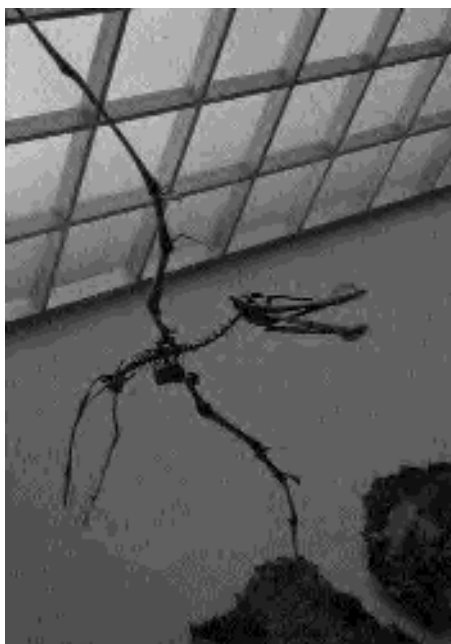


Figure 2. *Anhanguera*. Note how small the pelvic girdle is compared with the pectoral girdle. Notice also that the skull is longer than the body. Wing span ~5m. Photo Dino Frey.

crests look top heavy; but they are not - they are very lightly constructed. Nevertheless, it is the feeding end and pterosaurs needed an apparatus for catching food. They had to feed using only their mouths as their hands were attached to the ends of very long arms and their wings could not be used for manipulating food. All food gathering had to be done by the mouth.

Pterosaurs had a small pelvis; all the elements of the pubis are fused together as are the vertebrae of the sacrum forming a rigid box-like structure into which the rear limbs lock (Figure 2). This is the business end for landing. The vertebrae just behind the neck and through the thorax are all fused together, as are the adjacent ribs and the neural spines making it very heavily braced. The backbone is locked tight, also forming a very rigid box-like structure, with the shoulder girdle in which the lower two elements, the coracoids, are often fused to the upper two elements, the scapulae, forming a very rigid circular structure encasing the backbone on which to anchor a pair of wings.

There are generally a lot of similarities between rhamphorhynchoids and pterodactyloids, but there are a few small differences which are to do with the ratios of different components in the wing: for instance the metacarpal is very short in rhamphorhynchoids whilst in most pterodactyloids it is exceedingly long. There are some differences, probably related to flying manoeuvrability and speed, in the shapes of the humerus and especially in the skull, but essentially the body form is rather conservative.

Consider the gross morphology of the skull. There is a hole for the eye (the orbit); there is a hole in the skull in front of the orbit and there is another hole for the nostril (Figure 3). In pterodactyloids these two holes have merged together to make one big hole the nasoantorbital fenestra. This skull is full of holes and is constructed of a series of beautifully engineered thin bony struts. Cross-sections through the skull show it to be triangular and cross-sections through the individual struts are also triangular. The bone is very thin and is very light but also very strong; it does not flex, everything is locked tight. The lower jaw is one single



Figure 3. Close up of the skull of *Scaphognathus crassirostris* showing the holes in the skull and the widely spaced teeth. Photo Dino Frey.

long piece of bone. In a meat-eating dinosaur there is an articulation which allows for the absorption of shock when biting. Pterosaurs do not have this articulation so in this they differ from many reptiles. The eye was very large; that fits with an animal that is an active flyer, it surely needed to see where it was going, it needed to be able to see where its prey was so presumably had acute vision. They are assumed to have been pursuit predators or fishers.

Two holes in the back of the skull show that pterosaurs belong to a group of reptiles called the diapsids. Pterosaurs are not dinosaurs but they belong in a group which includes dinosaurs and crocodiles and that group is called the Archosauria. A lot of workers consider pterosaurs as the sister group to the dinosaurs, meaning that they are more closely related to dinosaurs than they are to crocodiles. Recently it has been suggested that pterosaurs lie outside the Archosauria and are not as closely related to the dinosaurs as previously thought. Yet another aspect of controversy in pterosaurs.

Let us consider the skull in a bit more detail. It has a large eye and the eyeball is supported by a sclerotic ring, there is the antorbital fenestra (with the nostril). In many pterosaurs with teeth the dentition is elongate and very widely spaced (Figure 3). Such teeth are no use for processing food in the mouth: prey was simply caught and swallowed, so the mouth is really a trap that took fish from the water. It was thought that they were biting the fish but then the fish would be impaled on the largest teeth and they had no means to get them off.

The skeleton of the arms of pterosaurs contain many elongate bones; on the humerus a delto-pectoral crest projects forwards operating as a lever for the attachment of flight muscles to the scapula above and the coracoids below which allows for vigorous flapping of the wing. The humerus is usually a short, very robust bone. It was thought that pterosaurs were purely gliding animals, but if this were the case, then they did not need a big strong delto-pectoral crest or the large sternum. All the rigid apparatus of the shoulder girdle is to facilitate large flight muscles, so pterosaurs were active powered flying animals: they could flap and actively take off from the ground.

The wrist is interesting because instead of having all of the elements of the wrist lying side by side they are end to end; so there is one element that is nearer to the body, a proximal carpal, and

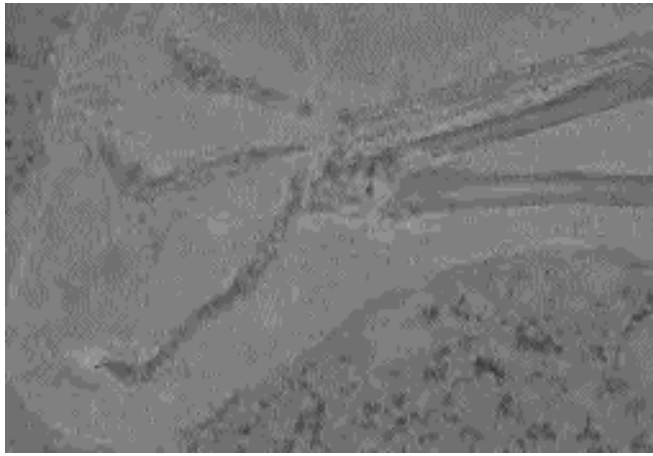


Figure 4. Detail of *Scaphognathus crassirostris* hand. The three clawed fingers probably had a web between them. Photo Dino Frey.

one that is further away, a distal carpal. There is also a little bone, the pteroid, attached to a lateral carpal, that sticks out of the front of the wrist. It is a controversial bone because nobody knows what it is. We do not know where the pteroid bone has come from; maybe it is a modification of one of the carpal bones; perhaps it is part of a digit. Some reconstructions show it projecting back towards the neck, while another reconstruction show it pointing forwards and down. In those reconstructions where it points towards the neck it is connected to a membrane which goes to the neck, thus increasing the surface area of the flight membrane. In reconstructions where it points downward it is considered that a much narrower membrane is attached extending along the front of the wing from the neck to the fingers which can be controlled like the front flaps on an aeroplane wing. The palm of the hand is composed of highly elongate metacarpals (Figure 4): three are like thin pieces of wire that connect to three small fingers, while a fourth is massive, with a large roller joint at the end. The fingers were not vestigial, they were being used for something, but they were short, and each had a good-sized, robust claw.

Now that leaves one more element: the main flight finger. This is the largest ever finger in the animal kingdom: in one specimen it can be almost 2.5m long; that is a very, very long finger (Figure 2). It consists of four elements and articulates proximally on the massive metacarpal with the big roller joint. This finger is a substantial component of the wing and is either the little finger or the fourth finger (which finger it is depends on how the pteroid is interpreted). In the literature most people say that it is the fourth finger which means that pterosaurs lost their little finger. But in that evolutionary model, the pteroid, a new element, has to be invented. If the pteroid is derived from a thumb then pterosaurs are flying with their little pinky finger which just got very long. Contrast that with birds. In a bird the fingers are substantially reduced to tiny little elements while the distal part of the wing is made up of the primary feathers. Pterosaur wings evolved from the arm and hand as they did in bats, but bats incorporated all five fingers into the posterior parts of the membrane. Pterosaurs incorporated the fingers into a very thin front strip of the wing membrane while the main part of the wing membrane stretches from the posterior-most finger down to the ankle (Figure 5).

Consider the legs of pterosaurs. They fit into a relatively tiny pelvis. They have a femur which, instead of being at ninety



Figure 5. *Quetzalcoatlus* - the largest ever flying animal with a wing span of over 9m. Notice that the wing membrane is only connected to the knee in this reconstruction. Most workers now believe that even in these large forms it connected to the ankle.

degrees to the body which would bring the legs nicely underneath the pelvis allowing an upright gait, the pterosaurs have it crooked at about forty-five degrees. Pterosaurs must have waddled if they walked bipedally like dinosaurs. However, evidence from biomechanics and from fossil footprints and trackways indicate that pterosaurs walked on all fours. The leg could go very far forwards, very far backwards and round and round. There was scope for considerable movement.

Several really good specimens of pterosaurs have the flight membranes preserved as impressions in fine-grained limestones: these specimens come from places like the Solnhofen Limestone in Germany and, in a different style of preservation from the Crato and Santana formations of Brazil. Such spectacularly preserved specimens demonstrate that the flight membrane was connected to the finger and extended all the way down to one of the toes. The flight membrane is similar to the bat in that there is a huge surface area between the fore and rear limbs which gives them a phenomenal amount of control as they could move their arms up and down, forwards and backwards and bend at the metacarpal; they could bend the distal part of the wing by bending the little finger backwards and they could control tension in the wing membrane by moving the legs. As they could also move the legs downwards they could also completely change the shape of the wing to slow themselves down and form a parachute. This also produced some problems because when they wanted to use their legs for landing, they had to couple the landing with controlled flight at the same time. Perhaps they could slow their flight to near standstill, and quickly lower the legs.

There remains considerable controversy regarding the flight of pterosaurs. It also took a little while before they were recognised as reptiles and, I think there must have been fifty or sixty years between the first discoveries of pterosaurs in the 1700s and Cuvier, in the very early 1800s, who declared that these animals were reptiles and were flyers. Even after Cuvier people doubted the ability of pterosaurs to fly. Now that it is accepted that pterosaurs could fly we argue about how they got off the ground, how much flying they did, whether they were active dynamic soarers (which they probably were) and how much flapping they

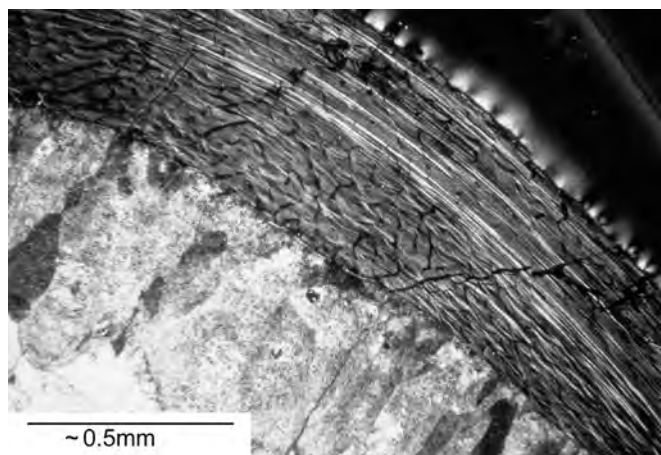


Figure 6. Thin section through a pterosaur bone. Notice the many thin layers arranged like plywood.

might do. More recent controversies are concerned with the legs and their walking ability. Did pterosaurs walk on all fours like bats or did they walk on two legs like birds? The great thing about being a bird is that your flight apparatus is independent from your back legs. You can do what you like with your back legs, it does not matter. If you are a swift you do not even use them, you just hang onto a rock face every now and then but mostly swifts spend all their time flying; they have tiny little back legs, they do not bother with them very much, they even sleep on the wing. Birds do not have the legs tied up with flight, they use them for landing or for walking and running, but pterosaurs and bats have their limbs locked into the flight membrane and this poses severe problems for locomotion on the ground. Some reconstructions of *Pteranodon* depict it as a biped standing on its hind legs. This arose when it was thought that dinosaurs were active animals rather than the slow lumbering beasts of the reconstructions of the pre 1970s. The reasoning being that if pterosaurs were related in any way to dinosaurs, as some believed, then they too must have had advanced physiologies and were probably bipedal as were theropods. So from the late 1970s to recent reconstructions of pterosaurs are often depicted as bipeds. Until recently few pterodactyloids had been found with unequivocal wing membranes preserved down to the back ankles. However, new specimens from Brazil show that their membranes connected to the ankle and these animals could not have been bipeds - they were quadrupeds. Pterosaurs walked around on all four limbs. Fossil footprints support this hypothesis.

In the Araripe Basin in north-east Brazil there are fossil mines and the people that work in the fossil mines dig out nodules of limestone that sometimes have three dimensional pterosaurs inside. I have seen a nodule containing a three dimensional skull. The miner who dug out the nodule wacked at it to see what was inside (no preparator would ever dare) and by a complete fluke it split right through the brain case. There are two massive optic lobes – that fits very nicely with those big eyes. To hunt fish from high in the sky acute vision is essential and large optic lobes would be required to process that visual data.

Is there anything to be learnt from the anatomy of pterosaurs? One thing they did was to evolve very large wings. Birds get pretty big but pterosaurs got much bigger. An albatross's maximum wing span is about 3m; the Cretaceous pterosaur *Quetzalcoatlus* had a wing span of about 12m (published estimates of 18m are wild

exaggerations). So a large pterosaur wing span of 9-12m is three times the wing span of the largest extant bird and is all supported by one long structure (the arm and finger) made of bone. Pterosaurs flew as small animals (juveniles) and got bigger and bigger and were always able to fly. So it is an advantage that bone is a material that can grow and always functions for the job that is intended. There are some things that have to be done to make the long thin elements light and strong and one of the things is to modify the cross-section.

Wings of pterosaurs have a variety of cross-sectional shapes according to the type and degree of stress to which they are subjected. Sometimes they have triangular or oval cross-sections and in some specimens the wing fingers have T-shaped cross-sections. A cross-section of pterosaur bone shows that the distance from the outer edge of the bone wall to the inner is considerably less than a millimetre. There are layers where bone has been added as reinforcement (especially in corners) and there are frequently a series of microscopically thin layers of bone laid down in different orientations, like plywood (Figure 6). It is these modifications of the bone that allow the pterosaur skeleton to be exceedingly thin, and therefore light, but at the same time exceedingly strong. Perhaps aircraft manufactures can exploit some of these designs.

Rhamphorhynchoid pterosaurs had long tails but they usually did not have head crests. On the other hand pterodactyloid pterosaurs commonly had very short tails and head crests and it seems that their crests were quite bizarre. *Coloborhynchus* (Figure 7) and *Anhanguera* (Figure 8) had a crest on both the premaxilla above and on the dentary below. *Cearadactylus* on the other hand had no crest. The function of pterosaur crests has been the subject of heated debate. It might have been related to feeding, stabilising it whilst flying with its lower dentary in the water, or perhaps for sexual display. There are some pterosaurs which even had multiple bony crests. It is now known some bony crests supported soft



Figure 7. Model of *Coloborhynchus*.



Figure 8. *Anhanguera* skull. Photo Dino Frey.



Figure 9. *Tapejara wellnoferi*. The bony crest at the front of the skull supported an even larger soft tissue head crest. Photo Dino Frey.



Figure 10. *Tapejara imperator*. Side view
Drawing by Julian Hulme.

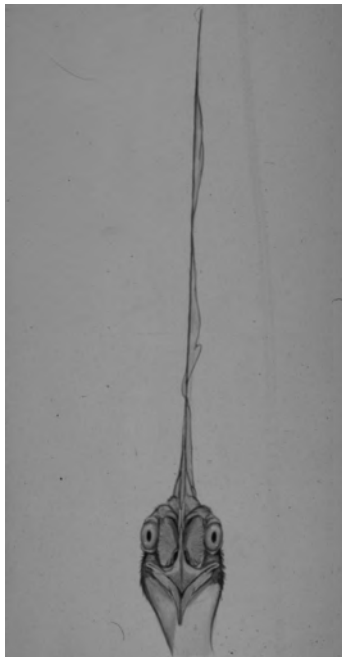


Figure 11. *Tapejara imperator*. Front view.
Drawing by Julian Hulme.

tissue crests, with the bony crest merely a support of a more elaborate structure (Figures 9, 10, 11). Some crests were sufficiently large to have had an aerodynamic effect – it might not have been useful, it might have been a hindrance, but nevertheless it would have had an effect. Rhamphorhynchoid pterosaurs have a little flag-like membrane on the end of their long tails which, when flicked, probably attracted their mates, but if you are a flying animal a long tail is a hindrance as it produces drag. Magpies are not as good at flying when compared to crows as they have long tails, but the long tail is good for attracting females. There have been experiments where birds that have long tails have been given even longer tails (by sticking feathers on the end) and found to be even more attractive to females, though much less efficient flyers. Pterodactyloids lost the long tail, so head crests were probably used in courting replacing the tail flag as an attractor or signalling device. They probably also had slightly more efficient flight because they got rid of the long tail.

As an aside: Isn't it nice when the toy industry invents prehistoric animals? This toy Pteranodon has teeth which makes it heavy (Figure 12); the toy industry invented the teeth of Pteranodon to make the toy look fierce. But Pteranodon does not have teeth - that is until two years ago when Dino Frey and I found a pterosaur which has a Pteranodon-like head crest and teeth in the jaws (Figure 13). So this animal was discovered by the toy industry before palaeontologists found a real one.



Figure 12. This toy 'pteranodon' has been given teeth. Such a pterosaur has now been discovered in the Cretaceous of Brazil.

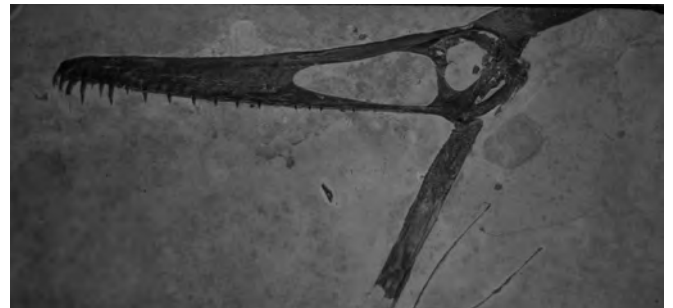
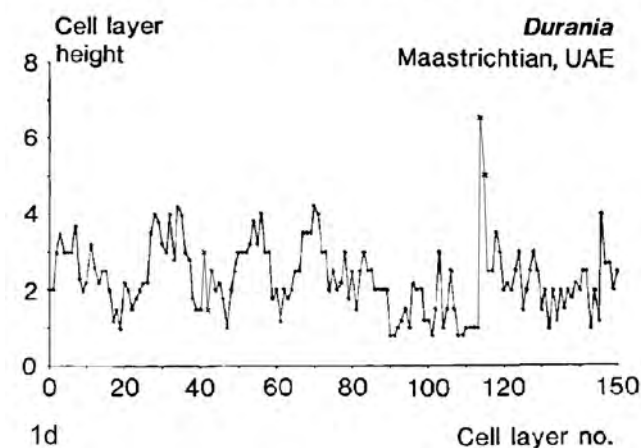
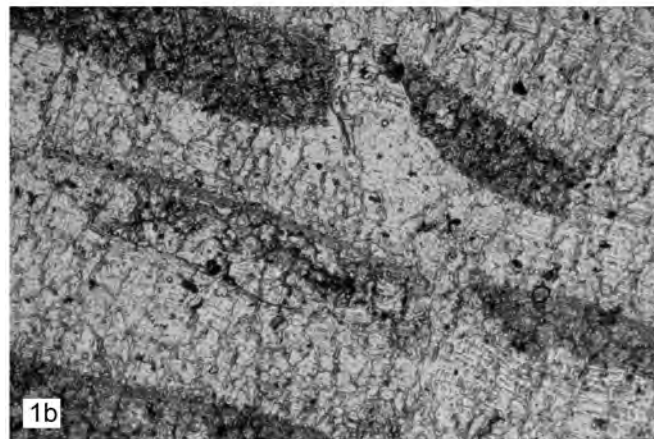


Figure 13. Invented by the toy industry this crested pterosaur with teeth has recently been discovered in Brazil.

Fossils as ‘smart particles’

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One of the fascinations of the geological record is its ability to catch the effects of momentary events that happened long ago, such as raindrops falling on mud beside a drying pond. The form and arrangement of sedimentary particles can tell us much about certain aspects of the environments in which they accumulated, especially the means of their transport and deposition, but are often mute on others. Take salinity, for example, which finds physical expression only in the extreme form of evaporites. An understanding of the ecological preferences of organisms, however, allows much sharper insights to be derived from fossils. Thus, we can be fairly confident that echinoderm remains, preserved *in situ*, indicate water of normal marine salinity, while frogs and newts record freshwater. Organisms are highly sensitive to a wide range of environmental variables, so, for the purposes of sleuthing the past, we might think of them as ‘smart particles’. However, as with all ‘high-tech gizmos’ we need to follow the instruction manual carefully to use them properly – and that means understanding their biology and taphonomy (style of preservation).

Fossil testimony may range from the virtually instantaneous, such as footprints on drying mud, to longer-term records, perhaps documenting entire life-times. The latter would include growth responses to ambient conditions. For example, specimens of the rudist bivalve *Durania* (Figure 1a), preserved in life position in beach conglomerates deposited around the proto-Oman mountains in the latest Cretaceous, show an outer shell layer structure typical of their family, the Radiolitidae, consisting of stacked layers of tiny cells (Figure 1b, c). We know from other radiolitids that the vertical cell walls formed by progressive building up of

Figure 1 (a) ‘Bouquet’ of specimens of the rudist bivalve *Durania* (Radiolitidae) preserved in life position in a vertical section of beach conglomerate of Maastrichtian age in Jebel Faiyah, UAE. Lens cap is 55mm across.

- (b) Photomicrograph of acetate peel from a vertical section through the cellulo-prismatic outer shell layer of the lower valve of another radiolitid rudist, *Biradiolites*, from the Santonian of Plan d’Aups, SE France. Top is up. Note the fine growth banding within the floors and walls of the cells (which here are filled by dark micrite). Width of frame is about 0.9mm.
- (c) Photomicrograph of vertical thin section through the outer shell layer of the lower valve of *Durania* from the locality in (a). Top is to the right. Note the periodic thickening and thinning (yielding the compact zones) of the cell layers, as well as the serpentinite grit incorporated within the shell, testifying to the turbulent environment. Width of frame is about 3.8mm.
- (d) Plot of the heights of successive cell layers in a vertical section of the outer shell layer of the lower valve of *Durania*, from the locality in (a), showing the periodic fluctuation in cell heights. The periods range up to about 26 cell layers, especially in the earlier formed part of the shell. Cell heights in arbitrary units.

ridges on the shell growth surface, and that each cell layer was built up from between fourteen and twenty-eight minor growth increments (Figure 1b). Such figures strongly hint at a semi-lunar (spring-neap) tidal cycle. So it is gratifying to find that the periodic thickening and thinning (to yield dense zones) of the stacked cell layers in the Omani *Durania* (Figure 1c) involve higher order cycles of up to about 26 cells layers (Figure 1d), which is just as

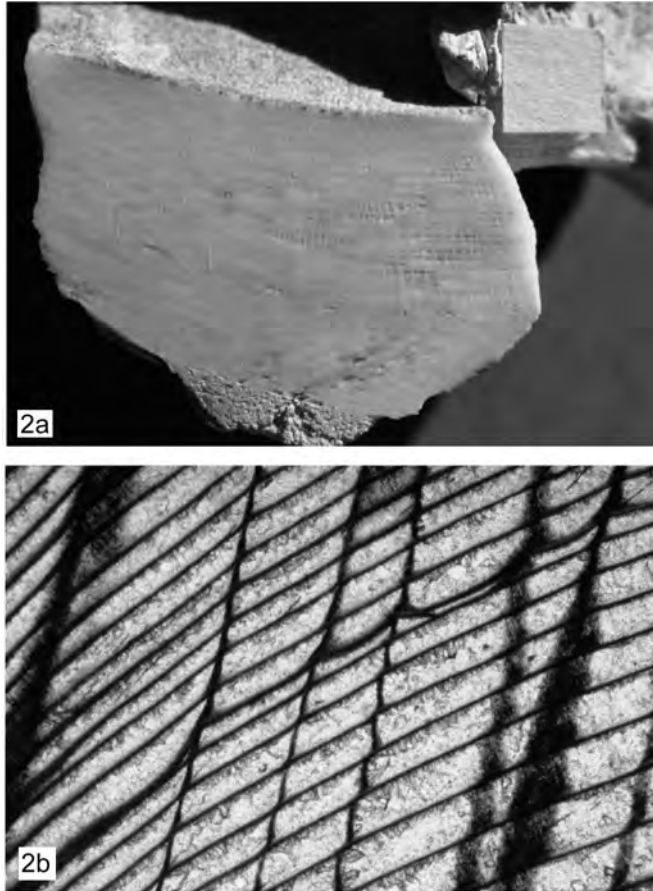


Figure 2 (a) Polished vertical section through the outer shell layer of the lower valve of *Durania* from the Upper Campanian of the El Aramah Plateau, Central Saudi Arabia. Top is to the right. Note the periodic growth halts, marked by thin white lines dividing the cell layers into groups of about 16-18. Square is 10mm square. [For S369 students, this specimen came from a locality only a few km along strike from that which is illustrated on the cover of 'The Cretaceous World'.]

(b) Photomicrograph of vertical thin section through the outer shell layer of the lower valve of *Durania* from the locality in (a). Top is up. Note the distinct growth halt about half way up the image, with a cell-floor layer draped over incomplete vertical walls from the previous cell layer. Width of frame is about 3.8mm.

we would expect for complete annual growth bands, showing some expression of seasonality.

By contrast, specimens of *Durania* of only slightly greater age from central Saudi Arabia, some 900 km behind the Arabian margin, show only 16-18 cell layers per presumed annual growth period (Figure 2a), each time culminating in a sharp growth halt (Figure 2b). This implies that they simply stopped growing for 8-10 weeks each year, presumably due to a strong seasonal fluctua-

tion in some factor(s) in their highly restricted environment, most likely salinity and/or temperature. This regular interruption of growth is probably an example of an ecophenotypic (non-genetically determined) character, as it is not seen in the *Durania* from the open marine deposits around the Oman Mountains.

Other, genetically controlled attributes of organisms, the products of longer-term evolutionary adaptation, can tell us about the habitual conditions experienced by species over many generations. An example is provided by 'platy' corals, which are common in many carbonate platform deposits of various ages. Just like the living platy coral, *Leptoseris*, which inhabits relatively dim waters at some 25 m depth today, the (unrelated) fossil forms contain adaptations such as projecting shelves (*pennulae*) on their septa as well as perforations through the septa. By analogy with the living form, these features can be interpreted as adaptations for supporting a greatly elaborated gastro-vascular cavity, which in turn would have allowed the meagre harvest from the photosymbiotic algae in their tissues to be supplemented by suspension feeding (Insalaco, 1996). In other words, such corals can be taken as witnesses to slightly deeper or murkier waters than those inhabited by most other types of shallow water corals.

Adaptation, the installation of favourable characters in populations as a result of natural selection, brings in the topic of evolution. Here, we see a kind of cumulative 'genetic memory' of the experiences of previous generations. Successive modifications become accreted onto one another in the body plans of organisms, though with the passage of time their original adaptive functions may be lost. The German palaeontologist Adolf Seilacher has graphically referred to such residual features as comprising the 'attic' of organic form. So our 'smart particles' carry two kinds of messages, the first concerning ambient conditions, as discussed above, and the second concerning their genealogical history, or phylogeny. It is important not to confuse these two kinds of message in interpreting past conditions. A banal example is provided by fossil mammoths' teeth. It would clearly be inappropriate to conclude that the deposits in which they occur must have formed in a hot climate, because the teeth are from some kind of elephant, and elephants today live in hot climates – but why is that an inappropriate conclusion? The answer is that recognising the 'elephantness' of the fossils informs us only about the evolutionary relationships of the beasts from which they came, i.e. the historical message mentioned above. Other attributes (long, shaggy hair, for example) would suggest, by analogy with other (unrelated) mammals, adaptation in this instance to cold conditions. That may seem rather obvious, but other, more subtle examples abound, to trip up the unwary. A little earlier we discussed adaptations in colonial corals. Too often, their fossils are uncritically interpreted to indicate warm, shallow, well-lit waters, yet this is by no means a safe generalization. There is nothing in their fundamental organization that restricts them to such environments. While many living corals do possess photosymbiotic algae in their tissues, limiting them to the photic zone, there are also many that do not have them. Indeed there are, today, extensive mounds at up to about 1000m depth around the North Atlantic, which have been built up largely by a colonial (but certainly not photosymbiotic!) coral called *Lophelia* [you can learn more about these weird and wonderful mounds from this website:

<http://www.geol.uni-erlangen.de/pal/> (click under ACES)].

Hence, when faced with the extinct rugose corals of the Palaeozoic, which differ in many respects from living corals, we need to be wary of drawing any generalized inferences concerning the environments in which they lived, to avoid 'the elephant trap' discussed above. Instead, we need to combine what we can infer from their sedimentological and palaeogeographical contexts with critical study of their specific adaptive attributes.

If palaeoenvironmental inferences based on taxonomic affinity are unreliable, you might be wondering why, for example, we can still be relatively confident that in situ echinoderm fossils can be taken to signal normal marine salinities? The answer is that some taxonomic groups, as part of their phylogenetic legacy, display

certain traits that apparently forever constrain the ecological horizons of their members. Thus, in the case of the echinoderms, it may be that their water vascular system simply cannot cope with the osmotic stresses of life in freshwater; certainly, there are no exceptions today from among this large and diverse phylum. However, such taxonomic generalizations should always be treated with caution, as one of the most predictable aspects of evolution is its ability to throw up unpredictable exceptions. The safest strategy for inferring past conditions from fossils, then, is the recognition of adaptive modifications of form that are closely convergent with those seen in living (but not necessarily related) organisms. An example would be the aerial pneumatophore tubes that project both from the *Stigmara* roots of the Carboniferous *Lepidodendron* tree and from the roots of living mangroves, in which they serve to supplement the oxygen supply to the water-logged root systems. This general approach has been exploited with considerable success by my colleague Bob Spicer in reconstructing past climatic regimes on the basis of analogies between the leaf morphologies of living and fossil plants.

On the other hand, the phylogenetic signals mentioned earlier can be very useful in other respects, for charting larger-scale or longer-term patterns, such as the effects of mass extinctions and palaeogeographical changes. For an example, I return to my own work on rudist bivalves. Some years ago, my colleague Paul Wright brought me some beautiful specimens that he had collected in southern Oman (one is shown in Figure 3a). I had no problem in recognising the three blunt infoldings of the outer shell layer in the lower valve and the distinctively puckered margin of that valve (along with other characters) as diagnostic features of the genus *Torreites* (Figure 3b). The surprising aspect was that *Torreites* had hitherto been generally regarded as endemic to the Caribbean region, although the Serbian palaeontologist Alexandr Grubić had, some years before, recorded its presence in the United Arab Emirates, in a publication that had not been widely circulated.

Given the unlikelihood that such close similarities in respect of several features had evolved independently in populations occupying the two areas (especially since other such examples then came to light), we were next faced with the task of identifying the connection between the two disjunct populations. No trace of the highly distinctive *Torreites* has been recorded in any of the carbonate platform deposits along the Mediterranean Tethys/Atlantic route between eastern Arabia and the Caribbean, despite the considerable amount of work that has been done on them. The alternative idea that such a shallow marine form could somehow have traversed the Pacific, between the two sites, might at first seem implausible. Yet Deep Sea Drilling Project (DSDP) work through the 1970s and 80s had identified fossils of shallow marine origin, and of Caribbean affinity, in ocean-floor sediments re-deposited from sea mounts that had apparently built up from the Cretaceous Pacific floor as a result of what was later to be called 'super-plume' magmatic activity. The trans-Pacific route thus offered a plausible connection between our two *Torreites* populations, after all, with the constellation of sea mounts lying between them serving as stepping-stones (Skelton & Wright, 1987). The phylogenetic message from the fossils thus fitted well with the DSDP evidence for extensive volcanothermal edifice-building in the Cretaceous Pacific – a nice case of consilience.

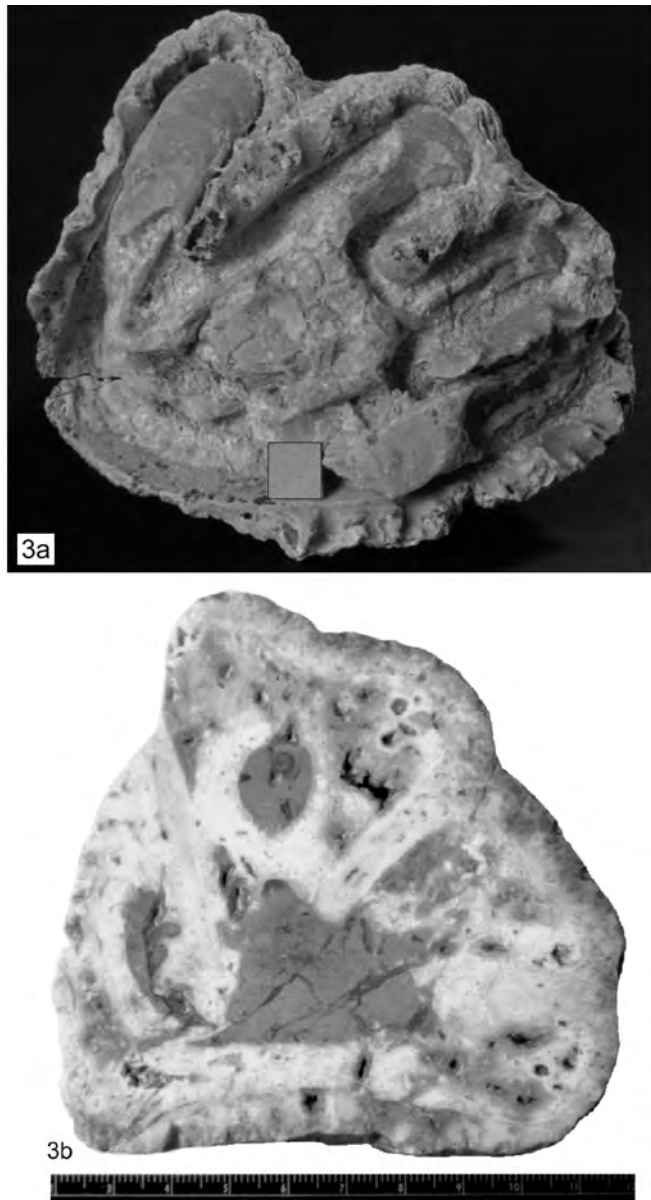


Figure 3 (a) *Torreites* from the Campanian of southern Oman, showing the operculiform upper valve seated in the conical lower valve, which shows distinctive blunt infoldings and a tightly pleated margin. Square is 10mm square.

(b) Section across the lower valve of *Torreites* from the Campanian of central Cuba. The same blunt infoldings as in (a) can be seen, albeit at different angles to one another, as well as the tightly pleated margin. Scale in cm.

So far, we have only considered what can be gleaned from the biological attributes of fossil organisms. However, their testimony does not cease with their death. The study of, so to speak, the 'death habits' of organisms (taphonomy) is a further rich source of clues. I won't dwell further on this aspect here, however, as Jane Clarke has done a beautiful job of this in her presentation.

The few examples that I have discussed illustrate some of the ways in which fossils can serve as 'smart particles' for reconstructing the past, ranging from what went on in ancient environments to major palaeogeographical changes. And, relative to many other methods of investigation these days, they're cheap to

use! So, cherish your palaeontologists, without whose testimony our understanding of the Earth's history would be very much the poorer!

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- Skelton P W & Wright V, 1987, A Caribbean rudist bivalve in Oman: island-hopping across the Pacific in the Late Cretaceous. *Palaeontology*, **30**, 505-529.

Book reviews

Architects of Eternity by Richard Corfield, 2001, Headline, 338pp, £18.99 (hardback) ISBN 0747271798.

The sub-title of Richard Corfield's first book is The new science of fossils, the founder of this new science, in the author's opinion, being T H Huxley. It was in 1868 that Huxley gave a lecture to the working men of Norwich at a meeting of the British Association entitled "On a piece of chalk" and illustrated his talk with fossils of planktonic foraminifera and coccoliths: it was this lecture that laid the foundations of palaeoceanography.

The 'old' palaeontology was all about the description and classification of fossils whereas the 'new science' is interpretation-based. It draws on other science disciplines, biology, physics, chemistry and geology, and depends on the very latest technology – scanning electron microscopes with secondary X-ray detectors, mass spectrometers, DNA sequencers and supercomputers but this book is just as much about the people who made the scientific and technical discoveries, and it is these people who are the 'architects of eternity'. Eternity in this sense is looking back to the beginning of life.

The author gives graphic accounts of important discoveries: the 19th century dinosaur finds in Wyoming and the antagonism between the collectors; the biostratigraphical research carried out using graptolites, ammonites and foraminifera; the advances in dating techniques; work using oxygen isotopes and the problems that had to be solved; the use of carbon isotopes and theories about the cyclicity of climate change; advances in molecular palaeontology and the search for a universal ancestor; pushing back the start of life on earth into the Precambrian with the research on the Burgess Shales; dating mass extinctions and much more.

Over the years there have been different theories of evolution proposed and opposed and there is a fascinating chapter in the book "The Savage Hand of Evolution" which starts with Richard Corfield's introduction to palaeontology while at Bristol University. He now directs the Stable Isotope Laboratory in the Department of Earth Sciences at Oxford University and, as he puts it "I have been exposed to ideas and techniques beyond the dreams of palaeontologists even 50 years ago."

No great knowledge of science is required to understand and enjoy this book and in the chapter about absolute dating for those who have forgotten their basic physics and chemistry he includes a primer about radioactivity.

At the end of the book there is a useful glossary of scientific terms and the Geological Timescale appears as an appendix. I found this a fascinating book and at £18.99 in hardback it is exceedingly good value.

Elizabeth Maddocks BA (Open)

A Field Guide to the Neogene Sedimentary Basins of the Almería Province, South-East Spain: International Association of Sedimentologists Field Guide by A E Mather, J M Martín, A M Harvey & J C Braga (eds), 2001, Blackwell Science, 350pp, £25 (paperback) ISBN 0632059192.

I've been to Almería twice. It is a fascinating and beautiful part of Andalucía and an exciting area to visit: metamorphic basement ranges like the Sierra de los Filabres form a framework for the Neogene basins around Sorbas, Vera and Almería. As a bonus there are some wonderful volcanics along the basin margins and in the Cabo de Gata, and colourful fault zones to "Ooh and Aah!" over.

The most beautiful countryside is protected as Natural Parks and Areas: fortunate, since much else is tomato and aubergine crops covered by hectares of plastic sheeting. The economically unfortunate desertification of the region is a boon to geologists who want to see the rocks in all their glory without getting rained on!

My first visit was on an OUGS trip led by Bill Gaskarth who has taken students there a number of times; the second was when I (perhaps rashly!) led a group myself, using notes from Bill's trip plus an earlier booklet on the basins also produced by Anne Mather together with Martin Stokes of Plymouth University. At the time I would have loved more detailed information and this book would certainly fill that gap.

Chapters describing various facets of the area: basin development, shallow marine sedimentation, marine to continental transition and the uplift, dissection and landform evolution of the Quaternary are illustrated by enough day and half-day field excursions to keep you busy for getting on for 3 weeks – it would take very little encouragement to get me on the next cheap flight to Almería or Alicante!

The content is well thought-out: good location maps, directions and grid references will get you to the right place despite the vagaries of Spanish maps, and detailed descriptions will tell you what you are looking at when you get there. There is practical information and plenty of background detail which, with the thorough referencing should satisfy the most inquisitive.

The format is fairly hefty, but firmly stitched and glued into its binding it should survive rough handling in the field.

As you can guess I think this is a book well worth using on my next visit, with one small proviso: as its title suggests, it is concerned almost exclusively with the basins so I hope there will soon be a companion volume covering the tectonics, basement rocks and volcanics of this area to supplement the 3 excursions described here.

Linda Fowler BA Hons (Open) OU tutor

The fate of the Neanderthals

Prof. Chris Stringer, Dept of Palaeontology, The Natural History Museum, London



Figure 1. The La Ferrassie Neanderthal (left) and Cro-Magnon skulls. Picture taken courtesy of Musée de L'homme, Paris.

About thirty five thousand years ago, there was a remarkable juxtaposition in Europe of late Neanderthals and early modern humans (Figure 1). Our main method of physical dating, radiocarbon, does not give us great accuracy during this critical period of time, but is sufficient to suggest that the two populations were broadly contemporaneous within regions, even if we cannot yet establish that they co-existed in the same valleys or even sites. This juxtaposition is also marked by what some archaeologists see as a major technological and behavioural revolution, one that occurred around the time modern humans arrived in Europe.

In my view, there is good anatomical evidence that Neanderthals and modern humans are more different from each other than today's human populations are different from each other, and that is as true when we compare Neanderthals and their approximate contemporaries as it is when comparing the skeletons of Neanderthals and recent humans. Ancient DNA recovery has helped significantly with interpretation of the morphological data because it is largely independent of it. Extracting authentic ancient human DNA has proved very difficult, but several

Neanderthals have yielded mitochondrial DNA, with four sequences (from three individuals) published so far. Although some workers have claimed the results are uninformative, or can be manipulated to support the view that Neanderthal genes survive today, the most straightforward interpretation of the data is that Neanderthals had their own, distinct, population variation, they diverged from the modern human lineage during the Middle Pleistocene, and they are now extinct (Figure 2). However, the Neanderthals were clearly very closely related to us, and neither the fossil nor DNA data rule out the possibility of some hybridisation between Neanderthals and modern humans, for example, during their period of overlap in Europe about 35,000 years ago. Such a species would have been very closely related to us genetically, and many comparable species of mammal can hybridise - for example, lions and tigers, dogs and wolves, even African and Indian elephants.

The real question is whether the species merged and, in my opinion, we have scant evidence of that for the Neanderthals and Cro-Magnons, since their core populations seem to have remained distinct. A putative hybrid child from Lagar Velho in Portugal has recently been described but, until more detailed studies are published, it is difficult to evaluate this claim properly. Nevertheless, such hybridisation could have occurred but the question remains on what scale and with what impact on later populations? A small degree of hybridisation could easily have been lost in subsequent demographic changes that geneticists have modelled for the Upper Palaeolithic from recent European mitochondrial and Y-chromosome DNA variation. For example, one recent study has suggested that most European mitochondrial lineages derive from post-Last Glacial Maximum population expansion.

However, whatever the outcome of these debates, recent research on Neanderthal behaviour certainly requires us to modify our views of their capabilities. The evidence seems compelling that they buried their dead, although claims that this was accompanied by flowers at Shanidar now seem suspect. Similarly, two separate

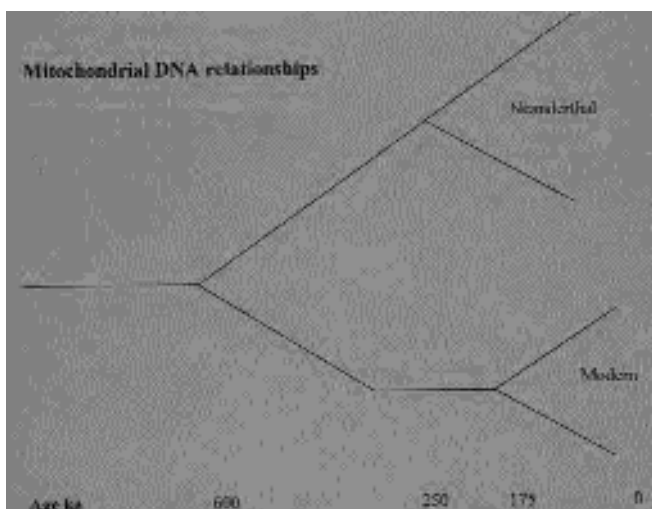


Figure 2. A schematic representation of the relationship of Neanderthals and modern humans, based on mitochondrial DNA data.



Figure 3. Reconstruction of Neanderthals in Gibraltar by Maurice Wilson. Recent excavations in Gibraltar have shown how well the Neanderthals had adapted to life on the Mediterranean coasts.

studies of a claimed Neanderthal flute from Slovenia suggest that this was actually the product of cave bear, rather than human, activity. However, finds made over 30 years ago at the French site of Grotte du Renne (Arcy-sur-Cure) suggest that some of the last Neanderthals made pendants from animal teeth. While some workers have questioned the stratigraphic integrity of the site, others accept the evidence, but interpret it very differently. Could the Neanderthals have done this independently, or only under the influence of neighbouring Cro-Magnons? And in contrast to the prevailing view that Neanderthals did not use marine resources, our excavations at Vanguard Cave in Gibraltar have demonstrated that their varied diet included marine mammals and baked mussels (Figure 3). Such complex behaviours show us that even if the

Neanderthals were not our ancestors, they were fully human. So when we come to consider Neanderthal extinction, we need to explore a variety of possible scenarios beyond rapid replacement, including a combination of resource competition from early modern humans (ultimately, but perhaps not immediately, derived from Africa), and the impact of repeated millennial-scale climatic fluctuations.

Further information:

Stringer C & Davies W, 2001, Those elusive Neanderthals. *Nature* **410**, 791-792.

HYPERLINK

<http://www.nhm.ac.uk/palaeontology/v&a/cbs/cbs.html>

Book reviews

An Introduction to Mineralogy by William D Nesse (University of Northern Colorado), 2000, Oxford University Press, 442pp, £27.50 (hardback) ISBN 0195106911

The book is in three parts:

- Part I: Crystallography and Crystal Chemistry
- Part II: Mineral Properties, Study and Identification
- Part III: Mineral Descriptions

There are three appendices:

- A. Effective Ionic Radii
- B. Determinative Tables
- C. Mineral Associations

There is a Mineral Index and also a Subject Index

The glossy plate beyond the indices shows an Interference Colour Chart

Inside the back cover is a useful copy of The Periodic Table

In Part I, containing five chapters, the concepts of symmetry, crystallography and crystal chemistry are presented with a clear text and a wealth of explanatory figures. I was quite tickled by the description of Glide Symmetry on P18, illustrated by alternating footprints and of Mineral Stability on P75, illustrated by books in stable, metastable and unstable positions. This section provides a good foundation for the chapters following.

Part II consists of five chapters describing the techniques and procedures, which any student would need for the study and identification of minerals. There are a few highlighted paragraphs, which may come in handy at revision time, including some useful questions. Perhaps more of these aides memoire might prove of interest. A reassuring assessment of problems, towards the end of the chapter, shows that difficulties do routinely arise but can be overcome with care and observation.

Part III has nine chapters and provides detailed descriptions of the most common minerals with added tables showing less common ones. Physical and optical properties are covered with descriptions of mineral occurrences in rocks and mineral deposits.

The content of the book provides a comprehensive text for teaching mineralogy to undergraduate students in the geosciences. The book is sufficiently extensive to be useful to a wide range of mineralogy courses, providing the specific knowledge of minerals needed by students. The book assumes that the students have background knowledge of physical geology and chemistry. Each section is reasonably self-contained. However, Part I provides a necessary introduction to chemical bonding and mineral structure, which is important to the understanding of the subsequent sections. The figures and their explanations are excellent. The two software programs "Shape" and "Atoms" were used to advantage in preparing crystal and mineral structure drawings.

At the end of each chapter is a helpful list of references and suggestions for further reading.

At £27.50 I would recommend this book to tutors and those students who could afford to buy it.

Patricia Tye, Retired Optical Microscopist/Mineral Separator

Soils of the Past by Gregory J Retallack, 2001, Blackwell Science, 404pp, £37.50 (paperback) ISBN 0632053763.

The book claims to cover 'a historical perspective on soil genesis and as a way of reconstructing the geological history of land surfaces on Earth'. It was written for advanced undergraduates studying soils and professional earth scientists. This is the second edition as the study of paleopedology has advanced so much in that time. It purports to provide answers to questions raised in the first edition. It is readable and informative. The first section begins fairly simply explaining plants and soil types for the non specialist but the other two parts are more technical. The diagrams look impressive but are not so easy to follow with Keys sometimes on other pages. It is American so many examples are from America but the author has included examples from around the world.

Soil is a 'complex zone of interaction between sediments or solid rock and the ecosystem or atmosphere' as defined by the author. The book is divided into three parts, then chapters but each chapter is subdivided and the page numbers given in the index.

Part 1 'Soils and Paleosols' covers paleopedology; soils on or under the landscape; features of fossil soils, soil forming processes; classification; mapping and naming paleosols; alteration of paleosols after burial.

Part 2 'Factors in soil formation' covers models; climate; organisms; topographic relief; parent material and time.

Part 3 'Fossil records of soils' covers a long term natural experiment in pedogenesis; soils of other worlds; Earth's earliest landscapes; early life on land; large plants and animals on land; afforestation of the land; grasses in dry continental interiors and human impact on landscapes.

Part 1 is fairly general. Apparently there are 17 distinct soil forming processes and even metamorphosed soils can be identified. Part 2 is very much what one expects in a teaching textbook. Part 3 starts with what we know about soils from other planets, Mars, Venus, Moon and meteorites. Chapter 17 makes interesting reading as Gregory Retallack would like to suggest that life began in soils but he does admit that little work has been done in this area. Could clays absorb organic matter then store and transfer this information? It sounds like science fiction but who knows. Mass extinctions in chapter 19 caused problems for plants by lowering 'biological productivity' but the greater problem is at the Permo / Triassic boundary.

There is a large glossary, but you do need to have a knowledge of paleosoil terminology to use it as the book is not written for the absolute beginner. A long list of references and an index complete the book.

Wendy Hamilton BSc (Hons), BA (Hons) Open

Dinosaurs: are they a metaphor for progress?

Dr David Norman, Director Sedgwick Museum, University of Cambridge

Dinosaurs have become the focus of considerable public interest in recent years, largely as a result of the Hollywood blockbusters such as "Jurassic Park" as well as the TV series "Walking with Dinosaurs". While interesting at one level (especially the sophisticated animation trickery that was used) the image that they simultaneously created about science, scientists and scientific activity ranges between being downright incorrect and the seriously misleading. This might be considered by many to be a matter of some desperation, given the overwhelming need for quality in our efforts to encourage the public understanding of science. I shall eschew these concerns, like Nelson with his telescope, and concentrate on real issues of dinosaur palaeobiology. This talk is devoted to explaining some of the work that has been done in the past, and is being done now, on real dinosaurs by real scientists in an effort to redress, albeit slightly, the balance between populist science-fiction and science. Developments within this admittedly narrow field of endeavour, when seen from the perspective of the present day, suggest that this area of research is as healthy and innovative as many other considerably younger branches of research

Historical threads

The agenda for palaeontology has always focused on the need to be able to use scientific understanding of living organisms in order to interpret, as accurately as possible, the biology, ecology, behaviour and evolutionary history of extinct forms of life (Norman 1985, Norman 1994). Ignoring earlier attempts to recognise the potential meaning and value of fossils, the subject really began to come of age at the close of the 18th century through the work of Baron Georges Cuvier in Paris (Rudwick 1997). In many respects a man born ahead of his time, Cuvier significantly developed the branch of comparative anatomy to the extent that his personal libraries of the illustrated and described anatomy of living species could be used as a reference point for the identification of all manner of fossil remains.

Among his more notable achievements, within the scope of this talk, were his recognition of the existence of fossil remains of genuinely extinct creatures; his work (along with Alexandre Brongniart) on fossil elephants proved beyond doubt that extinction was the fate of many species. Equally important was the demonstration of the existence of extinct gigantic fossil creatures utterly unlike those living today. His recognition of the giant, extinct, aquatic, lizard-like creature *Mosasaurus* is paramount among these discoveries. Cuvier's ability to show that this fossilised animal was a giant extinct relative, quite unlike any modern lizard, opened up entirely unexpected possibilities for fossil collectors: notably the opportunity to discover creatures of an entirely new type (some gigantic) and reveal evidence of times in Earth history that were entirely unlike the present day.

Within a relatively few years after the work of Cuvier was published gigantic, extinct denizens of the past began to make their appearance. Canon William Buckland, who had been appointed to a Readership in Geology at Oxford in the 2nd decade of the 19th century was the first to formally describe the remains of one of these gigantic creatures from England. These were collected

from a slate quarry at Stonesfield (North Oxfordshire); however, it should be recorded that Buckland was himself heavily dependent upon a visit by Georges Cuvier to Oxford. He, no doubt, assisted Buckland with the interpretation of the bones that had come to light. In 1824 (Buckland 1824) these bones were christened *Megalosaurus* (on the basis of the fossilised teeth and bones of what appeared to be a land-living "giant lizard" from Oxford). Within a year another giant lizard had been described (Mantell 1825). Gideon Mantell, a practicing physician (but enthusiastic – in truth an obsessive fossil collector in his spare time) described *Iguanodon*, a giant herbivorous fossil lizard from the Wealden of Sussex. Again the interpretation was heavily reliant upon consultation with Georges Cuvier, and what emerged, based on a few scattered teeth and bones, was a gigantic extinct relative of the living iguana (hence the chosen name for the fossil).

Such extraordinary discoveries excited considerable interest in the scientific world, and greatly encouraged interest in the field of fossil research (the name "palaeontology" was not invented until the 1830s) and in a more general way in the ancient history of the Earth. Further discoveries of material of *Iguanodon* in the 1830s gradually padded out the idea of the form of this animal, particularly as a result of the discovery of a partial skeleton near Maidstone known, rather touchingly, as the "Mantel-piece" (Norman 1993). The bones were pieced together using the living iguana skeleton as the template in true Cuvierian fashion, and seemed to suggest a lizard of truly staggering proportions. Depending upon which bones or teeth were used the animal could be estimated to have had a body length of anywhere between 100 and 200 feet (~30-65 metres).

The interest generated by such discoveries was intense, and resulted in a huge increase in the number of discoveries of fossil remains in Britain in particular. By the late 1830s Gideon Mantell was publishing beautifully illustrated popular books summarising many of his own discoveries; these revealed a previously unknown world of animals and plants in Britain. The artist John Martin was able to depict this "antediluvian" world in a frontispiece of Mantell's "Wonders of Geology" (Mantell 1838), the entire landscape in this piece was populated by creatures and plants discovered by Mantell from the Wealden of Sussex.

However things were about to change, and quite dramatically so, with the emergence of a quite brilliant anatomist from London – Richard Owen. Though later reviled, largely for his political chicanery, and his vehement opposition to Darwin's 'new' theory of evolution in the late 1850s, his early contributions to science, and palaeontology in particular, should not be overlooked.

During the late 1830s Richard Owen was provided with a grant to research and review the discoveries of British Fossil Reptiles to date. The results of this work were published in 1840 (largely the marine reptiles) and 1842 (terrestrial forms). These reviews were masterly pieces of work for the time. One singularly important set of observations (Owen 1842) concerned the group of large fossil reptiles (including *Megalosaurus*, *Iguanodon* as well as the lesser known *Hylaeosaurus* that had also been described by Gideon Mantell from the Wealden of Tilgate Forest). These creatures he

singled out for special consideration because of their size and peculiarities of anatomy, and created a new category of fossil reptile: the dinosaur. Owen demonstrated that these animals were very distinctly different from any living land-dwelling reptile because of their great size (far surpassing even the largest lizard) and their ability to walk with their legs arranged pillar-like beneath the body, rather than sprawled out to the sides. In many ways Owen's dinosaurs anticipated in their body form, the features seen in modern large mammals (such as elephants). In fact Owen went so far as to suggest that his dinosaurs were representatives of a time in Earth history when reptiles filled the ecological niches filled today by the large tropical mammals. Owen even speculated about dinosaurian physiology in ways that were extraordinarily prescient when viewed in the light of the (dare I say ... heated) debates in recent years concerning the metabolic status of dinosaurs (Norman 1994).

Owen's dinosaurs were eventually brought to 'life' through the building of the Prehistoric Park surrounding the Great Exhibition when it moved from Hyde Park to Sydenham and was re-erected in 1853/4. To this day Owen's dinosaurs can be viewed on their artificial islands in Crystal Palace Park, South London, as perpetual testaments to Owen's extraordinary vision (McCarthy & Gilbert 1994).

That Owen's vision, based as it was at the time on precious few scraps of bone and teeth, was at fault is hardly surprising as was shown by later discoveries. By an extraordinary piece of good fortune a remarkable cache of dinosaurs was discovered in Belgium in the late 1870s (Norman 1987). These remains were discovered in a clay pocket that interrupted a commercially mined coal-seam in the Mons Basin at the small coal-mining village of Bernissart. At first regarded as pieces of wood, because of their fibrous texture and dark brown colour, it was soon realised that the remains were actually fossil bones, and some teeth also recovered showed that these creatures were very similar to Gideon Mantell's *Iguanodon*. Further careful excavation at the site revealed a veritable Aladdin's Cave of dinosaur skeletons. Over thirty partial or complete skeletons were recovered over the next 6 years, and taken to the Royal Museum of Natural History in Brussels for study by their resident scientist Louis Dollo. Careful examination and eventual mounting of numerous skeletons showed that Owen's original vision of *Iguanodon* – immortalised in 1854 – was substantially incorrect (Norman 1992). Dollo gave the creature a kangaroo-like posture in accordance with its bodily proportions and in strict adherence to the anatomical principles advocated by Cuvier almost a century earlier. This pose is the one still seen today in nearly every museum that has a cast of this famous old dinosaur (even my own!).

Updating earlier work

Revisiting the well-studied *Iguanodon* as a PhD student in the late 1970s it became apparent that the Dollo reconstruction itself contained a few unexpected errors, whose origins could be traced all the way back to Cuvier. To a considerable degree the modelling of the skeletal pose of *Iguanodon* relied upon the body proportions exhibited by the preserved skeletons: the combination of long neck, powerful arms with clawed hands, stout chest, long back legs and a long tail found no better comparison among living animals than the kangaroo (or wallaby in Dollo's case – it was probably the only skeleton that was accessible to him at the time). So it is not surprising that the dinosaur itself is shown in the kanga-

roo resting pose. Assessing the skeleton a little more carefully it became apparent that the posture of the animal could not have been as proposed by Dollo, it was actually a physical impossibility that required the tail to be physically broken. What emerged was a posture in which the backbone was held more horizontally, and the forelimbs were used, at least occasionally, to assist in walking, rather than being held permanently clear of the ground (Norman 1980).

Glancing back momentarily at Gideon Mantell's "Mantel-piece" with the knowledge derived from a far better understanding of the total anatomy of *Iguanodon*, it is clear that this amazing specimen, discovered in 1834, had the potential to advance the understanding of dinosaur anatomy by several decades. Displayed on the slab of Kentish Rag are the tell-tale anatomical proof of its ornithischian affinities (1887) and its body proportions (1882), but hindsight is an irrelevant form of wisdom in relation to scientific investigation as a whole (Norman 1993).

Another intriguing historical quirk to emerge more recently is another connection between Richard Owen and the clearer understanding of dinosaurian anatomy and posture. The now infamous 1854 dinosaurs at Crystal Palace were superseded as early as 1859 by the discovery in North America of a new, partial dinosaur named *Hadrosaurus* by Joseph Leidy of Philadelphia (Norman 1985). This discovery included some teeth (rather similar in overall shape to those of *Iguanodon*) and both front and back legs; these latter showed clearly that the front legs were considerably shorter than the back ones, and suggested an upright and more kangaroo-like posture, thus anticipating Dollo's reconstruction of *Iguanodon* by two decades. As a result of this and other more dramatic events, the interest in dinosaur studies rapidly shifted across the Atlantic as the exploration of the US mid-West began to reveal incredible dinosaur riches as the fabled "bone-wars" of E D Cope and O C Marsh flared between the 1870s and 1890s (Desmond 1975).

However less well known is another amazing coincidence (Norman 2000b). In 1858, just as Joseph Leidy was picking over the bones of his new dinosaur from Haddonfield in New Jersey, Richard Owen was presented with the almost complete skeleton of a robust, armoured dinosaur that had been dug from the cliffs at Charmouth, near Lyme Regis in Dorset. Over the next few years Owen described this dinosaur in some detail. The extraordinary thing, in retrospect, is that Owen made so little of this new and, probably equally exciting discovery – this was, after all the first virtually complete dinosaur ever discovered. He described its anatomy, discussed a little of how it might have lived, but no more, none of the sweeping interpretations or powerful insights that characterised his earlier work. Had he wished to, he could easily have 'proved' that his Crystal Palace dinosaurs were not so flawed after all. The new dinosaur *Scelidosaurus* was armoured and very similar in build and proportions to Mantell's Tilgate Forest creature *Hylaeosaurus*, and the reconstruction of the low slung, spiky-backed, quadruped is as correct as might be reasonably expected given the information that Owen had at his command in the 1840s. It is again strange that as vain and proud a man as Owen did not chose to trumpet the correctness of his Crystal Palace vision in this instance. But it seems likely that his institutional responsibilities and political commitments made it impossible for Owen to devote time to the science that he was trying to practice in the interstices of his increasingly congested diary.

***Iguanodon* revisited**

Iguanodon was one of a large group of herbivorous dinosaurs and proved to be an interesting animal to investigate simply as a means of trying to understand what it actually means to be a herbivore. Herbivory is generally apparent from the general shape of the teeth of an animal and the shape of its skull; both have to be modified in order to cope with the stresses associated with a diet of generally tough, fibrous plants. The teeth tend to be in general blunt and often chisel-shaped, or specially modified to allow for a grinding motion that allows tough plant fibres to be pulverised to aid more efficient and speedier digestion and assimilation. The skull has to anchor muscles that can exert great forces on the skull, which must therefore also be heavily reinforced, and the jaws are usually arranged to increase the leverage that the jaw muscles can exert on the food between the teeth (Norman 2000a).

Iguanodon shows a number of clear herbivorous features in its skull. The front of both upper and lower jaws are toothless and were covered in life by a tortoise-like keratinous beak, which is ideal for nipping off vegetation. The teeth are arranged in parallel ranks, and are chisel-shaped to aid the cutting of plant fibres, and there is strong evidence for the presence of fleshy cheeks that would have allowed these creatures to chew their food repetitively (another essential if the aim is to really pulverise what you are eating). The skull is strongly constructed and the lower jaw has a large lever-like coronoid process to increase the forces that can act on the food when the jaws close. However, what emerged from detailed analysis of the jaw motion was the existence of a curious bilateral hingeing of the sides of the skull that would allow the upper jaws to move sideways as the lower jaws closed. This unique system, which I dubbed pleurokinesis (Norman 1984), is now known to exist in a wide range of these types of herbivorous dinosaurs, and allowed them to generate a complex and powerful grinding motion that mimics the jaw action seen in well-adapted herbivorous chewers of the present day (such as the hoofed or ungulate mammals) (Norman & Weishampel 1985).

Developing an appreciation of the herbivorous abilities of dinosaurs leads naturally to a consideration of the relationship between herbivores and the plants that they eat and the larger scale patterns exhibited during the evolutionary history of both animals and plants. Such approaches are being used to examine the degree to which the evolution of land plants (notably the origin of the angiosperms, which occurred during the Early Cretaceous) at a time when the pleurokinetic ornithomimid dinosaurs were themselves diversifying (Barrett & Willis 2001).

New frontiers, new challenges

Recent technological innovations in fields un-related to palaeobiology are also capable of providing data relevant to dinosaurian investigations. Computed tomography (CT) scans, which have been widely applied in the field of medicine, have been used with some success on fossil material. Such techniques allow the internal anatomy of skulls to be investigated in ways that were impossible until recently and have been used to examine the respiratory passages in the skulls of crested duckbilled dinosaurs (Sullivan & Williamson 1999), as well as the structure of the endocranial cavity and pneumatic cavities found within the skull bones of theropods.

An alternative approach to the use of such data is represented by recent work on the well-preserved skull of the dinosaur *Allosaurus* (Rayfield *et al.* 2001) has demonstrated how 3D infor-

mation generated by CT scans can be used to generate finite element meshes that simulate the complex structure of a dinosaur skull. Adding the material properties of bone, cartilage and tooth enamel allows the behaviour of a dinosaur skull to be reconstructed when subjected to the stresses associated with feeding. Such work is capable of determining the range and variety of stresses to which the skull is best adapted, and can lead to predictions about the feeding behaviour of dinosaurs, and other aspects of their palaeobiology, such as social behaviour (Rayfield, Norman & Upchurch 2002).

Systematic techniques have been considerably refined over the past two decades through the development of a variety of computer-based numerical methods, such as parsimony-based cladistics (PAUP). These techniques generate patterns of relationship between taxa that can be tested statistically. These approaches have greatly increased the objectivity associated with systematic analysis and can be used to generate phylogenetic trees that form the basis of examining the nature of character acquisition associated with patterns of evolutionary change over time (Smith 1994).

The evolutionary history of dinosaurs is, however, also unusually interesting because of the time in Earth history when they lived. The tectonic setting of the Earth's continents during much of the Mesozoic Era was dramatically different from the present day. The earliest dinosaurs appear in Late Triassic times when the Earth's continents were still locked together in the form of the supercontinent Pangea. During the Jurassic, as dinosaurs began to radiate in an evolutionary sense, the supercontinent of Pangea began gradually to fragment. As an inevitable consequence populations of dinosaurs became isolated on individual continental land-masses. In a very general evolutionary sense isolation of once communal populations (allopatry) is regarded as one of the primary mechanisms by which evolutionary change is generated. Looked at on a continental scale it seems probable that there may be broad-scale correlations between the pattern of continental fragmentation and the evolutionary history of the organisms, such as dinosaurs, whose populations were subject to similar fragmentation. The search for such coincident patterns at distinctive periods of time in Earth history (focusing on the Mesozoic as a test case) has begun and is generating interesting results (Upchurch, Hunn & Norman 2002).

Finally GPS techniques have recently been used profitably to study the trackways left by a variety of dinosaurs in Oxfordshire (Day, Upchurch, Norman, *et al.* 2002). Such work has provided valuable insights into the locomotor techniques employed by different dinosaur taxa under different conditions, and has provided novel insights into the style of locomotion used by theropods when moving at different speeds (Day, Norman, Upchurch, *et al.* 2002). This work is about to be followed up by detailed digital mapping of footprints in order to investigate more thoroughly the interaction between parts of the foot and the sediment during the generation of each print.

A word or two in my defence

Dinosaur palaeobiology has undergone steady development since the Dinosauria were first defined by Richard Owen in 1842. While the work during the 19th century was confined primarily to comparative anatomical and functional observations, linked to consequential taxonomic revisions, the work during the 20th century has shown an increasing tendency to incorporate develop-

ments seen in other branches of science. This had led to an increase both in the breadth and intellectual depth of investigations that are now possible. In many ways the approaches being adopted today increasingly mirror some of those used by forensic scientists. The rather crude analogy that I have drawn in the past between the style of investigation (centred on the body at the scene of a crime) that are employed by present day forensic pathologists on the one hand; and the type of approach needed by palaeontologists (in the investigation of a newly unearthed fossil skeleton) and the variety of scientific disciplines that have to be incorporated into such investigations on the other, is considerably less trite than it used to be.

So, rather paradoxically, the animals that have so often been used as the definitive symbol of conservatism and an inability to change, have spawned a branch of scientific investigation (dinosaur palaeobiology) that is quintessentially vibrant, synthetic and accustomed to change.

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Book review

Classic Landforms of the Antrim Coast by B Smith & P Warke, 2001, Series Editors - C Green, M Naish and S Naish, Geographical Association, 52pp, £8.95 (paperback) ISBN 1899085475.

This book is one of sixteen titles in print or preparation covering classic landforms of the British Isles. It is intended for educational parties and the public in general, as such it is written in an easy manner using the simple format of a house, roof to basement, to assist in visualising geological time. The introduction provides a good overview of the areas to be visited and the important features that can be seen. It starts by introducing tertiary dykes, moving down through the Cretaceous chalk, Lias clays and finally the basement rocks, dykes and faults. Sea-level change and coastal erosion are discussed in a simple manner.

Each location is clearly explained both by word and diagram and cover such topics as slope instability, rotational slip, fault controlled topography, igneous intrusions, and effects of wave energy, formation of dune systems, and the classic Giant's Causeway. The manner in which the guide is written is in keeping with the aims of both the Geographical Association and The British Geomorphological Research Group "to provide concise, simple and informative guides to help students and visitors to a better understanding and therefore appreciation, of the landscape."

The book's clarity and format makes it a very easy tool to use in the field and as a winter's night reading. At £8.95 the book may be priced out of the casual purchase market but is good value for money if you are intending to visit the region.

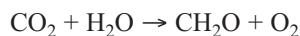
Paul Wyre continuing Earth Science Student

Carbon dioxide and the evolution of plants

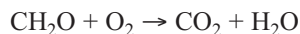
Professor Bill Chaloner, Royal Holloway, University of London

Carbon dioxide and the biosphere

Carbon dioxide, which is a very minor component of the atmosphere at between 0.03 and 0.04%, is none the less the source of the carbon in the organic matter of virtually all terrestrial life. Plants, including algae and blue-green bacteria, take up carbon dioxide from the atmosphere, and using light energy in the process of photosynthesis fix the carbon from the air and convert it to a range of organic substances: carbohydrate, lipids and (with nitrogen from the soil), protein. In the process they release oxygen. The complex of green pigments referred to as chlorophylls, together with other pigments, are the essential catalysts in the process of photosynthesis. A very simple version of this quite complex series of photosynthetic reactions can be expressed as:



where "CH₂O" is a generalised formula for carbohydrates such as glucose (C₆H₁₂O₆). All animal life depends directly on this process of "primary production" as its source of food, either as herbivores eating the plants directly, or as carnivores, getting the foodstuffs second-hand by eating the herbivores. Beyond this, the vast range of decomposer microorganisms and pathogens, bacteria and fungi, live on these organisms, their dead tissue or their excrement. They use this productivity of plant photosynthesis as a source of organic matter for growth of their own tissue, but much is broken down in the process of respiration to provide energy, consuming oxygen and releasing carbon dioxide into the atmosphere. The formula for this process is the exact reverse of that of photosynthesis:



Thus the entire working of the terrestrial biosphere hinges on the uptake of carbon by photosynthesis from that very minor component of the atmosphere, and its eventual return as carbon dioxide, released by respiration, from a wide range of consumer organisms, including of course mankind.

The fact that carbon dioxide has received much attention in the last decade results from its being one of the most important of the "greenhouse gases" in the atmosphere. This means that carbon dioxide, like water vapour (but unlike the other major atmospheric components such as oxygen and nitrogen) helps to retain the heat energy re-radiated from the Earth in response to radiant energy received from the sun. This "greenhouse effect" in fact helps to maintain the earth's temperature at something over 20°C above that (very low) temperature that would be sustained if we did not have an atmosphere with such greenhouse components. Concern has been widely expressed that the well-documented rising level of carbon dioxide in the atmosphere will cause an enhanced greenhouse effect, and that this will produce "global warming". The preoccupation, both in scientific circles and in the public perception, with the perceived undesirable effects of such global warming, has led to the current trend in political correctness to refer to carbon dioxide as a "pollutant". A normal requirement of a pollutant is that it causes harm, either to human health or the environment. It is rather absurd that an atmospheric component

which is so absolutely vital to the continued existence of life on Earth should be labelled in that way!

In addition to this terrestrial cycling of carbon, there is, of course, an equally important cycling taking place in the oceans. Photosynthetic phytoplankton carry out carbon fixation in the uppermost, illuminated zone of the sea and this marine primary productivity is then consumed by zooplankton and thence by plankton feeders (mostly eating both plant and animal plankton) so feeding ultimately all marine animal life from protozoans to whales. Of course there are connections between terrestrial and marine carbon cycling in that, for example, much organic detritus is carried off the intertidal wetlands into the sea, where it helps to feed the littoral fauna. But both the terrestrial and marine biota share the same carbon dioxide, which is in equilibrium between the air and that dissolved in the ocean.

The rising carbon dioxide level

For those of us interested in changes in the global environment over the course of geological history, it is appropriate to look more closely at what is happening to carbon dioxide at the present time. The monitoring through the year of the carbon dioxide level, first carried out on Mauna Loa in the Hawaiian Islands and subsequently at many widely dispersed sites, first alerted mankind to the steady rise, year on year, that is taking place (see e.g. Francis & Daise 1997). This steady rise is generally attributed, with good cause, to the burning of fossil fuel, itself produced by photosynthetic primary production in the geological past, but long since taken out of circulation as buried carbon. This global rise of carbon dioxide is one of the most securely documented processes in the whole spectrum of "global environmental change", which includes among others such changing parameters as the mean global temperature, the mean sea level, the extent of the "ozone hole".

In addition to this steady rise, there is also an annual fluctuation, most noticeable in Northern hemisphere sites (this being the hemisphere where the greater part of all terrestrial vegetation is situated). Each winter the CO₂ rises to a peak which falls off the following summer as terrestrial vegetation starts up its most active phase of photosynthesis, "drawing down" the atmospheric CO₂. As the winter sets in and much of the higher latitudes are snow-covered and deciduous trees have lost their leaves, photosynthesis slows down. But respiration by animals (and plants) and most especially by microorganisms breaking down litter in the soil, continues even if at a reduced rate. But overall, there is a steady increase in the winter peak year on year. These fluctuating roles of photosynthesis and respiration through the seasons remind us of the constant involvement of the biosphere in the level of carbon dioxide in the air.

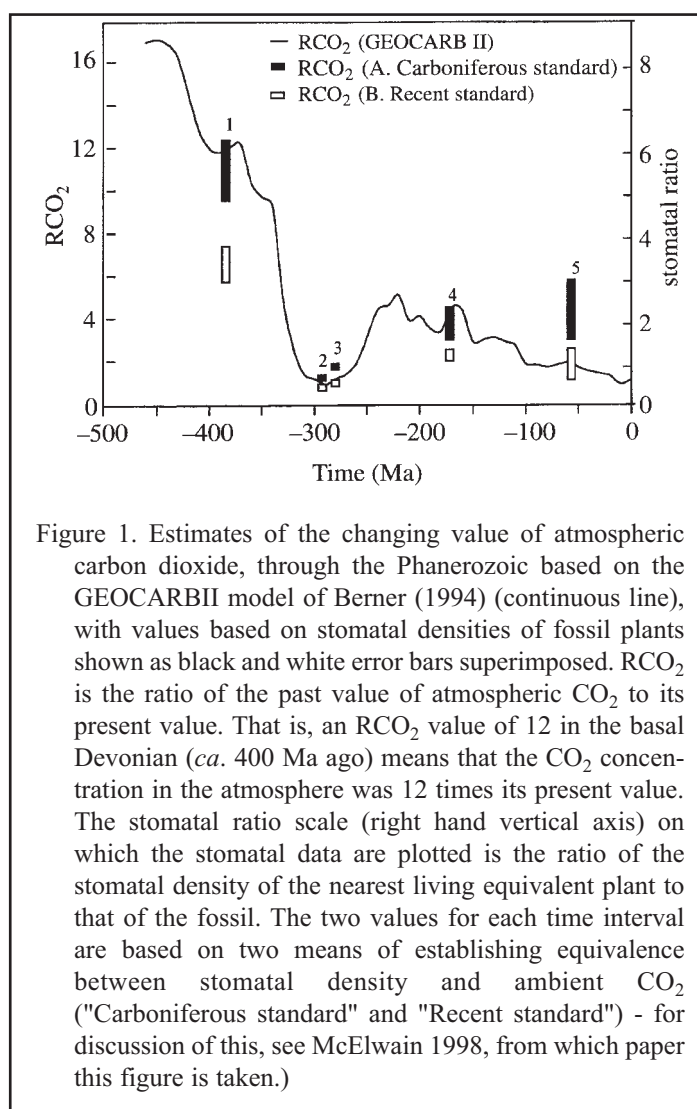
Past changes in carbon dioxide

The changes in atmospheric composition that we can see happening today can be traced back in time, at least for the latter part of the Pleistocene by studying the atmosphere trapped in ice cores in the Antarctic and Greenland ice caps. This was first attempted by

Russian workers coring the Antarctic ice at their Vostok station (see e.g. Francis & Dise 1997). Ice cores, representing the accumulated and compacted snowfall over the icecap, show clear annual banding, comparable to those of tree rings, so that the air trapped in each successive year can be extracted and analysed, and the age of each band can be counted back from the present surface. Further, the oxygen isotopes in the frozen water give a measurement of the regional temperature in the area from which the sea water evaporated to give that precipitation. This gave a curve initially extending back some 120,000 years (through the last glacial phase and the previous warm interglacial period). Later work has carried this record back through four glacial/interglacial oscillations which shows how the carbon dioxide level in the atmosphere paralleled the regional temperature; high carbon dioxide coincided with the warm phases, low with the glacial conditions. This was one of the most telling pieces of evidence that the phenomenon of a carbon-dioxide-led greenhouse effect seemed to be causally involved in the climatic oscillations of the last million years; and hence that rising carbon dioxide now spelt impending global warming.

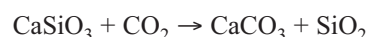
To follow the long term changes in carbon dioxide throughout the course of geological history, we need to look to more indirect "proxies" of atmospheric composition. It is the very widely held view of earth scientists that the early Earth's atmosphere was rich in carbon dioxide and probably lacking in any free oxygen. There is mineralogical evidence from the degree of oxidation of iron minerals, and the stability of reduced minerals such as iron sulphide in detrital deposits, that through the course of the Precambrian, the atmosphere became progressively oxygenated, and the carbon dioxide content fell. We have the first evidence of stromatolites, structures comparable to those formed by photosynthetic bacteria at the present day, from about 3,500 million years ago, and it is from about this time that evidence of oxidation of the atmosphere becomes progressively stronger. It seems likely that the photosynthesis of these early photoautotrophs was the cause of this progressive change in the global atmosphere; that the fixation of carbon by photosynthesis was taking carbon out of the atmosphere and burying it as carbonate or detrital organic matter in marine sediments with release of oxygen. If this interpretation is correct, then the oxygenation of our present atmosphere is the result of this ancient photosynthesis.

Robert Berner (1998) has had sustained interest in the changes in atmospheric composition through geological time, and particularly through the Phanerozoic, which he has reconstructed in his several "Geocarb" models. These use a range of sources of evidence, including calculations based on the total amount of carbon buried at any point in the geological past as carbonate, coal and other forms of sedimentary carbon. The fractionation of stable carbon isotopes in both ancient soils and ocean floor sediments also carries a signal of the contemporaneous atmospheric carbon dioxide. From these and other sources Berner has plotted a curve of changing carbon dioxide through the Phanerozoic (Figure 1; see also Francis & Dise 1997). The first striking feature of this curve is the remarkable fall-off of carbon dioxide from the Silurian through the Carboniferous. This was the period of the establishment of plant life on land, which undoubtedly must have had a powerful effect on the rate at which photosynthetic carbon fixation took place, with increasing rate of carbon burial through the coal accumulation occurring from the late Devonian through the



Carboniferous. Although there were subsequent major fluctuations in global carbon dioxide the level never reached the pre-land-plant levels of the Lower Palaeozoic, which Berner estimates at between 10 and 20 times the present level.

There is another way in which plant life was involved in the major fall in carbon dioxide through the Devonian and subsequently. It has long been known that carbon dioxide reacts in a soil profile with minerals containing calcium silicate (of which calcic feldspars are probably the most abundant) dissolving the calcium as calcium bicarbonate, which is water soluble and so may be leached from the soil profile and carried by the drainage system eventually into the oceans. The insoluble silica remains in the soil. The calcium bicarbonate in the oceans is the primary source of calcium carbonate used by organisms from foraminifera to corals, ammonites to bivalves, to make their shells or other hard parts. The effect of this process is that atmospheric carbon dioxide ends up as biogenic carbonate being buried in ocean sediments and so "taken out of circulation", at least in the short term. A simplified formula for the totality of this process may be given as :



The involvement of land plants in this process is in greatly accelerating a mechanism which must have been initiated long before plant life was established on land, namely the interaction of atmospheric carbon dioxide and calcium silicates. The roots of

plants penetrating the soil have a major role in not only mechanically extending the soil depth, but in carrying carbon dioxide (produced by respiration) down the soil profile. With their death the roots then add to the decomposing organic matter in the soil, which then generates carbon dioxide from microbial respiration. The increasing size and extent of land plant root development through the course of Devonian time is well documented by Algeo & Scheckler (1998). This silicate weathering role of plant roots has been studied by Moulton & Berner (1998) who have shown that the transport of calcium and magnesium ions from a weathered bare igneous rock surface may be five times greater where that same rock exposure has been colonised by vascular plants. That movement of calcium and magnesium is, of course, also a measurement of the movement of the bicarbonate ions which accompany them, and hence a measure of the carbon fixation occurring at the rock surface. The fall in atmospheric carbon dioxide through the Devonian and early Carboniferous in Berner's curve (Figure 1) may therefore be attributed not simply to photosynthetic fixation of carbon, but also the increasing role of silicate weathering accelerated by the evolution of land plant rooting strategies.

Among other interesting features of Berner's curve is the fact that the two low levels of carbon dioxide, the Carbo-Permian and the Pleistocene, correspond with the two major glacial phases of the Phanerozoic. This again gives support to the idea that in some way, at least, the carbon dioxide-driven greenhouse effect is implicated in global climate change.

Plant responses to changes in atmospheric carbon dioxide levels

We have good evidence from the fossil plant record that as the carbon dioxide level in the atmosphere has changed, plants have responded to that change in interesting ways. But to follow this part of the story we need to look at how land plants (as distinct from seaweeds) actually take up carbon dioxide in their photosynthesis.

There are a number of very evident adaptations to terrestrial life that are shown by land plants (vascular plants) which are not shown by plants such as algae living in an aquatic environment. These include a covering of cuticle, a film of waxy material which retards the loss of water by evaporation through the plant surface; for land plants obtain their water supply through roots in the soil, and for them it is a hard-won commodity to be conserved! With this largely gas-proof coating, the only route for carbon dioxide into the chlorophyll-rich tissue of their leaves is through a series of gas exchange pores in their epidermis, appropriately called stomata (mouths). Large numbers of stomata are present on the lower surface of most land plant leaves, commonly in excess of a hundred per square millimetre of leaf surface (the so-called stomatal density). Examples of fossil stomata are shown in Figures. 2a & b. Plants take in carbon dioxide from the atmosphere through their stomata, and this diffusion occurs simply because that gas is being consumed by photosynthesis within the plant tissue. A gradient is set up, from the (already very low !) carbon dioxide level outside, to the (even lower) level inside the air spaces within the plant. Of course oxygen diffuses out through the same stomata, at least when the plant is illuminated.

The other gas which passes freely through stomata is water vapour, and its loss through the stomata is called transpiration.

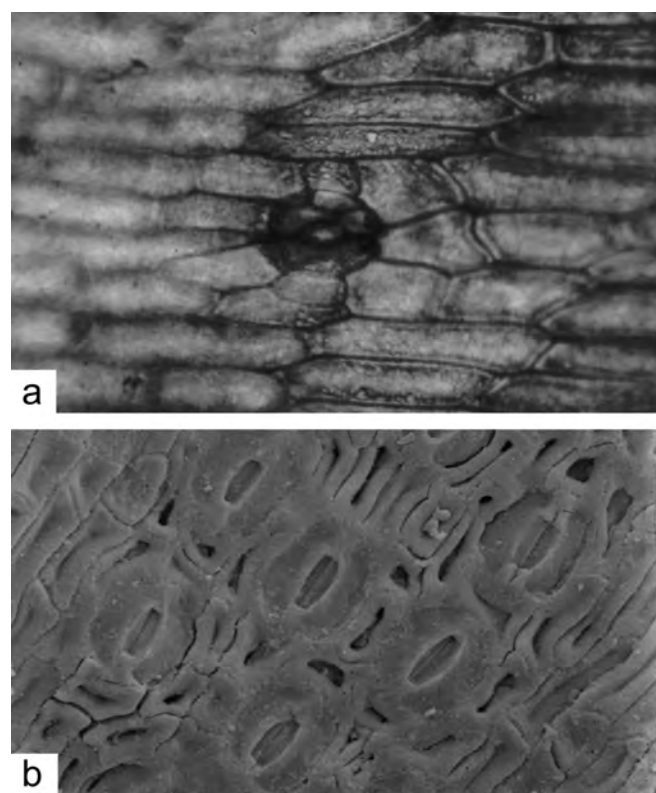


Figure 2. Surface detail of two fossil plants showing their stomatal density. (a) *Rhynia*, a Lower Devonian vascular plant preserved in 3-D in chert; a single stoma, emphasising the low density of stomata on these early land plants growing at a very high carbon dioxide level. Width of frame 240µm. (b) *Swillingtonia*, an early conifer, from the Upper Carboniferous, preserved as charcoal; the under side of a leaf, showing the closely crowded stomata comparable to those of many present-day conifers. The high stomatal density is attributed to the much lower concentration of CO₂ in Carboniferous times, compared with the Devonian (see Figure 1). Width of frame 110µm.

This loss of water is an inevitable accompaniment to keeping the stomata open for carbon dioxide uptake. For the most part plants can take up sufficient water through their roots to cope with this transpirational water loss. But of course this means that they need a water conducting system, the xylem tissue, of minute pipe-like cells which transport water from the roots to the leaves of land plants. The presence of xylem is a further characteristic feature of land-adapted plants.

Plants control the access to their inner tissue via their stomatal pores, as two guard cells on each side of the pore can open or close it. Under illumination, when photosynthesis is occurring, the stomata will normally be open, but they will be closed in the dark. Equally the stomata may close when under dry conditions the water loss exceeds what can be drawn in by the roots, and the plant is in danger of wilting. A typical temperate plant may lose about 200 molecules of water through its stomata for every molecule of carbon dioxide that it manages to turn into carbohydrate!

Woodward (1987) was the first scientist to investigate how the stomatal density of British trees had been affected by the rising carbon dioxide of the last hundred years or so. He did this initially by counting the stomata on leaves which had been collected

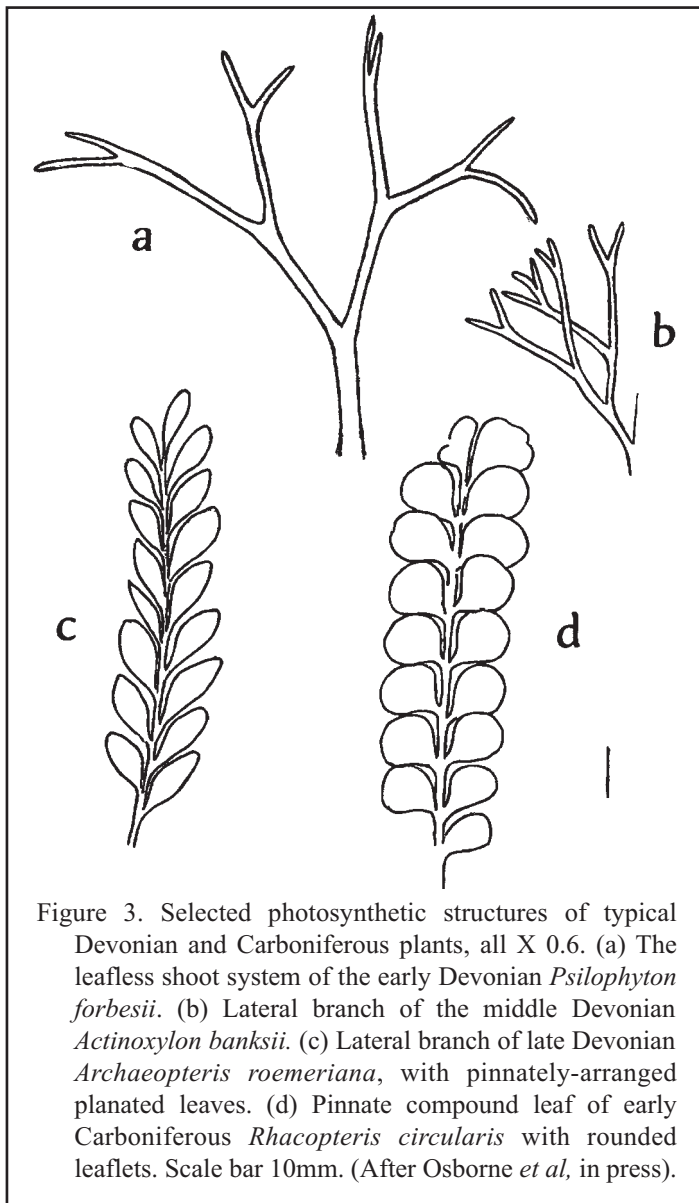


Figure 3. Selected photosynthetic structures of typical Devonian and Carboniferous plants, all X 0.6. (a) The leafless shoot system of the early Devonian *Psilophyton forbesii*. (b) Lateral branch of the middle Devonian *Actinoxylon banksii*. (c) Lateral branch of late Devonian *Archaeopteris roemeriana*, with pinnately-arranged planated leaves. (d) Pinnate compound leaf of early Carboniferous *Rhacopteris circularis* with rounded leaflets. Scale bar 10mm. (After Osborne *et al*, in press).

and pressed many years ago, extending back to the mid-18th century. Although the actual stomatal density was different for the several trees that he studied, they had all changed in the same direction and largely to the same extent. As the carbon dioxide has risen, the number of stomata has been reduced; that is, the stomatal density has fallen. If you take the present day value as 100%, on all the trees he studied, the stomatal density of the pressed leaves of 200 years ago for each species is about 140% of its present value. Further, Woodward showed that if tree seedlings are grown under lower carbon dioxide than we have at present, at the level known from the ice cores as the value 200 years ago, the same higher stomatal density is shown by leaves which have actually been developed experimentally in that low-carbon dioxide atmosphere.

This response of stomatal density to the carbon dioxide level demonstrated by Woodward in living plants was a clear invitation to palaeobotanists to see how stomatal density has changed over the course of geological time, and to compare it with Berner's carbon dioxide model. Jenny McElwain and I embarked on a study of fossil plants where, in those relatively rare instances where stomata are preserved, their density can be measured. (McElwain

& Chaloner 1996). It had long been known that the early vascular plants have very sparse stomata (growing at the time when, as we now know from Berner's curve, the carbon dioxide was ten to twenty times its present level). Most Palaeozoic plants are, of course, long extinct, so that there is no living counterpart to be compared with them as in Woodward's study. We adopted the only available strategy in these circumstances, which was to make a crude comparison with the "nearest living equivalent" plants, as closely related to the fossil as possible and of comparable habitat. This gave a series of values of approximate carbon dioxide levels which could then be placed on Berner's curve (Figure 1, and McElwain 1998, where details of this procedure are given). As that figure shows, the Palaeozoic and Mesozoic carbon dioxide values from stomata show reasonable agreement with Berner's, although the Tertiary values show greater divergence.

There is another aspect to these stomatal data, beyond their acting as an indicator of carbon dioxide levels. The fact that fossil plants show this kind of response to changing CO₂ levels has its own intrinsic interest. For it means that plants were responding in their development, and ultimately in their evolution, to changes in the environment (the CO₂ level) which they themselves had brought about, at least in the Silurian through Carboniferous interval.

Carbon dioxide and the evolution of leaves

When plants showing the characteristic adaptations to life on land first appear in the fossil record they are structurally very simple and unlike the majority of living plants. At the Silurian/Devonian boundary, from various parts of the world, we find small (2-3 cm high) branching plants of the genus *Cooksonia*, with stomata on the surface and a strand of water conducting tissue (xylem) at their core. Some of the branches end in swellings containing spores, and we believe these functioned like the spores of most living ferns in effecting reproduction of the plants. None of these early land plants have leaves, and we assume that these forking, cylindrical stems with their stomata functioned as the photosynthetic organs (Figure 3a). The great majority of early Devonian fossil plants are of similar morphology, although they become progressively larger through the course of the Devonian. By mid Devonian time, plants were producing lateral branch systems of cylindrical, forking, structures (Figure 3b); these were of limited ("determinate") growth and were the forerunners of the larger leaves which were to become increasingly common by the close of the Devonian and early Carboniferous (Figure 3c&d). This evolution of what are called megaphyll leaves (derived from a lateral system), which characterise the bulk of modern, living plants, has been well documented. The sequence of events which took place through the Devonian is shown in diagrammatic form in Figure 4, the stages of leaf evolution being set out in the "telome theory", first advanced by the German plant morphologist Zimmermann in the 1930s (restated in revised form in Zimmermann, 1959). This envisages a lateral branch on a simple forking vascular pant becoming "overtopped" by the other fork of the axis growing on past it and leaving it as a branch of limited growth (an incipient leaf) as opposed to the continued growth of the other arm (an incipient stem). The lateral branch system then becomes flattened in the horizontal plane to maximize light reception (so-called planation) and the flattened branch eventually evolves a "webbing" of tissue between the branches to complete the adaptation to a laminar leaf, like that of some modern ferns. In general terms, this sequence of events is well borne out by our

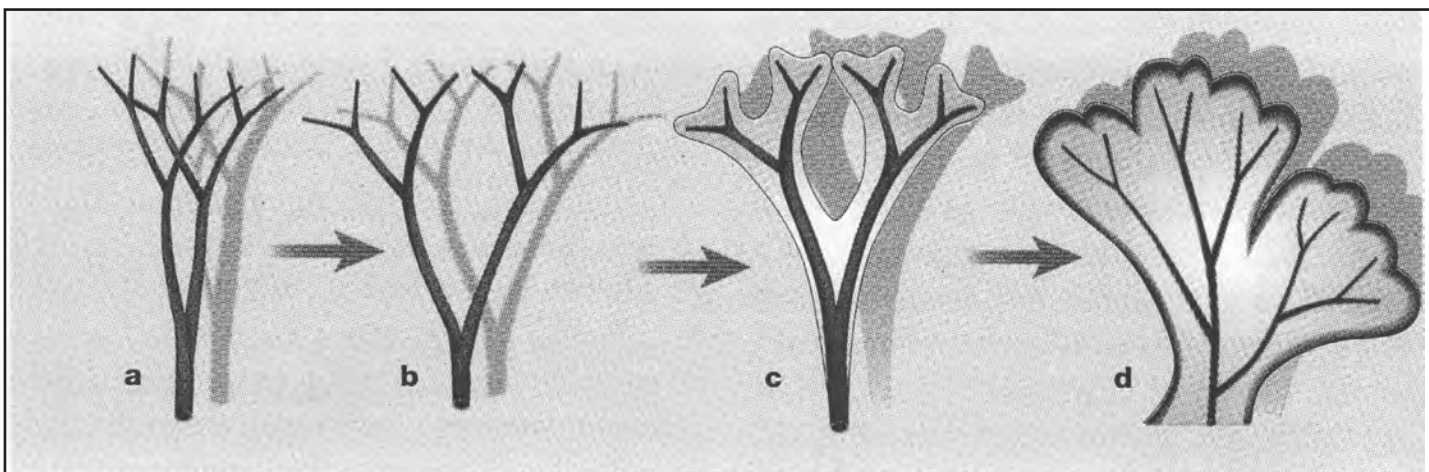


Figure 4. The origin of the megaphyll leaf, showing the progression from (a) a leafless branching axis, through flattening ("planation") of a lateral branch (b) (here shown in its entirety), and the subsequent "webbing" (c) between the branches to produce a laminate leaf with a branched venation system (d). This evolutionary sequence took some 40 million years, as the high CO₂ level of early Devonian time made the planated leaf less photosynthetically efficient than the cylindrical axis. As the CO₂ fell, so the planated megaphyll leaves came to largely supersede the early Devonian type of structure. From Kendrick (2001). Reprinted by permission from Nature, 410 (6826) p.309 fig. 1, copyright 2001 Macmillan Publishers Ltd.

record of fossil plants through the course of the Devonian. Examples of the relevant parts of typical Devonian and Lower Carboniferous plants are shown in Figure 3.

It is appropriate to point out here that there is another type of leaf which appears early in the fossil record, which had a different evolutionary origin; these are microphylls, the minute spine-like leaves of the club-mosses (Lycopods) which have a single vascular (xylem) strand running in to them, and which appear to have arisen early in the Devonian or late Silurian as direct outgrowth of the stem surface. They characterise this group of plants, the lycopods (which include the Carboniferous tree, *Lepidodendron*) in which the leaves remained as narrow structures, with a single vascular strand, throughout the evolutionary history of the group. Modern lycopods share this feature. But here we want to concentrate on the megaphylls, which typically have a branching vein system, which characterise the modern flowering plants and ferns.

The only puzzling feature of the evolutionary sequence set out above, which gave rise to the megaphyll leaf, is that it took so long for megaphyll leaves to evolve! Nearly forty million years elapsed (the span of the Devonian period) between the appearance of simple vascular plants and the general adoption of megaphyll leaves in several unrelated vascular plant groups (excluding the lycopods) by early Carboniferous time. Why did they take so long to adopt this seemingly more efficient means of photosynthesis? One obvious possibility is that some external constraint made the megaphyll leaf ineffective in the early Devonian; the one environmental feature which we know to have changed significantly through that period is the carbon dioxide. I speculated that while the carbon dioxide was some ten to twenty times its present level, the upright green photosynthetic cylinders of early Devonian plants, with their very sparse stomata could have been perfectly adequate photosynthetic equipment. It was perhaps only when the carbon dioxide was drawn down to close to its present level that plants were driven not only to greatly increase their stomatal density, but also to make thin plates of photosynthetic tissue, so shortening the length of pathway for the gas diffusing from the outside

to the photosynthetic cells.

I turned to colleagues at Sheffield University, David Beerling and Colin Osborne, with whom I had worked on stomatal density. They are of the school which believes that the best way to understand a biological system is to model it and then observe the reaction of the system to changing the variables. They showed that the length of the diffusion pathway into the leaf is a very small element of the many factors controlling the rate of photosynthesis. However, the changing stomatal density through the Devonian had other implications than those I had expected. They were able to show (Beerling *et al.* 2001) that the upright cylinder with its low stomatal density would indeed have worked well in the high carbon dioxide greenhouse world of the early Devonian; but had those plants had lateral megaphyll leaves, with the same stomatal density, the very low transpiration rate that they would have would result in overheating. The megaphyll leaf only became a practical proposition when the falling carbon dioxide raised the stomatal density, increasing the transpiration rate, and so effecting a cooling of the leaf tissue under full irradiation. The details of the model and the effect of stomatal density on the transpiration rate are set out in that paper.

So it now appears that the origin of the megaphyll leaf was held back by the high carbon dioxide; only as the plants themselves collectively drew it down through the course of the Devonian did the megaphyll become the most effective photosynthetic structure. (Leafless, green photosynthetic stems can still be seen in a few plants of arid habitats, where those particular environmental factors have driven them to it). It appears that in the origin of the leaf, as with the stomatal density, the plants changed the environment and then had to adapt to the very changes that they themselves had brought about.

One might speculate that there is a rather tenuous parallel here in the changes that mankind has brought about in the global environment and his capacity to adapt, socially and economically, to those changes. I hope we may be able to do it as gracefully, and a lot more rapidly, than the plant kingdom did!

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Book reviews

Strata: How William Smith drew the first map of the Earth in 1801 and Inspired the Science of Geology by John L. Morton, 2001, Tempus, 160pp, £9.99, (paperback) ISBN 0752419927.

At first I was attracted by the front cover - a striking layered spine contrasted with delicately coloured map extract from the General Map of Strata 1801, blended with a picture portrait of William Smith himself. I was also attracted to find out more about this man who was writing about geology at a time of few roads, sailing ships, the beginnings of railways and Industrial Revolution, and a time when there was a huge gap between the educated, rich landowners and ordinary people. I was not disappointed!

This book is very readable and charts William Smith's life and times in great detail. How he came into surveying by joining Edward Webb's business and graduating from small field surveys to coal mines and canal building. Through these activities he became very familiar with the stratigraphy, the lie of the land and the flora associated with different rocks. The first chapter is well illustrated with photographs of the houses in which he lodged while carrying out his surveys around Bath and Somerset, Tucking Mill House which he owned and extracts from his diary. Smith's stratigraphical expertise and knowledge spread as he was asked to travel to solve drainage problems in other parts of the country. The second chapter is also illustrated with extracts from Smith's writings on drainage and paragraphs from the biography on Farey, Smith's 'friend' who effectively gave away his geological findings.

Rivalry to his ideas, the culmination of his work and subsequent financial crises are documented in flowing, easy to read chapters, supported by noteworthy evidence from a variety of sources. I found the entries from John Philip's (Smith's nephew) Memoirs of William Smith particularly enlightening as here we glimpse the man himself. At the end of the book are useful appendices listing Smith's fossil species, his publications and manuscripts and a William Smith trail, complete with grid references.

I recommend this book to everyone. Morton's style of writing and frequent illustrations, both graphic and textual, ensure an informed read and have brought to light the strength of character and determination of William Smith. At £9.99 this book is very good value for money as a holiday read or one for your bookshelf. It will definitely be on my Christmas list!

Sue Hughes BSc Hons (Open)
continuing MA student

Igneous Petrology by Myron G. Best & Eric H. Christiansen, 2001, Blackwell Science, 458pp, £29.50 (paperback) ISBN 0865425418.

This book is written as an undergraduate text book. It is clearly written and has plenty of good diagrams and photos. It has the unusual idea of beginning each chapter with a list of fundamental questions, helping you to appreciate the aim of the chapter. It covers much of the igneous material of S339 and much more beside. One of the books recommended as further reading in S339 was by M.G. Best and I presume that this is the same author as this book.

Rather than the traditional chapter-by-chapter treatment of rock suites it is arranged mostly by process, which I think is a better way of organising the book. According to the authors of the books "overarching themes are the dynamic interactions between matter and energy and the ways in which transfers and transformations of gravitational and thermal energy drives changes in rock-forming systems".

The book covers composition and classification, an introduction to thermodynamics and kinetics, volatile fluids, phase diagrams, kinetics of crystallisation and resulting fabrics, the properties and behaviour of magma bodies, and field relations of intrusive and extrusive rocks. It then goes on to consider magma generation and differentiation and relates this to tectonic setting; however this is little over a quarter of the book. There is a glossary of 670 words.

There is a section on diapirs which surprised me. I thought that the concept of diapirism was being abandoned as thermally and mechanically unfeasible. The book is in agreement that plutons do not extend downwards for great distances but are tabular in form. But as regard mechanisms of ascent it mentions that there is controversy but comes down firmly in favour of diapirs rather than dyke-like sheeting facilitated by shear zones and faults.

I think it would make a nice book to have on hand as a reference for all matters concerning igneous rocks or for hard rock enthusiasts who would like to know more without getting too bogged down with technicalities as the authors have attempted not to make the maths too intimidating.

Susan Larkin B.Sc.(Hons), M.Sc.,
continuing earth science student.

Palaeodetective

Jane Clarke, MPhil (Open)

All palaeontologists are palaeodetectives as they have to extract information from fragmentary fossil remains. Initially they attempt to reconstruct the morphological detail of the organism and then try to deduce its mode of life. When all that is available is just one bone, or leaf frond, or just an impression, the results can be somewhat problematical.

Geologists are also palaeodetectives as they try to reconstruct conditions in which rock strata are laid down. Some beds are easier than others; some reveal their entire history whilst others only reveal the later stages.

All sediments undergo diagenetic changes due to heat and pressure during burial but mudstones in particular change more than most. Analysing mudstones reveals the diagenetic processes which have taken place since de-watering as de-watering usually obscures what has gone before.

This research, carried out as part of a Master of Philosophy with the Open University (Clarke 1993) has found a way to open a window into this hidden period using the vertebrate fossils contained within the mudstones. So, in this instance, fossils are being used as Time Machines.

The bones themselves only provide limited information. During diagenesis the fresh bone (hydroxyapatite $\text{Ca}_{10}(\text{PO}_4)_6(\text{OH})_2$) undergoes neomorphic (atom for atom) replacement: phosphates are replaced by carbonates and fluorine while the hydroxyl radical is replaced by fluorine resulting in carbonate-fluorapatite which is a very stable substance.

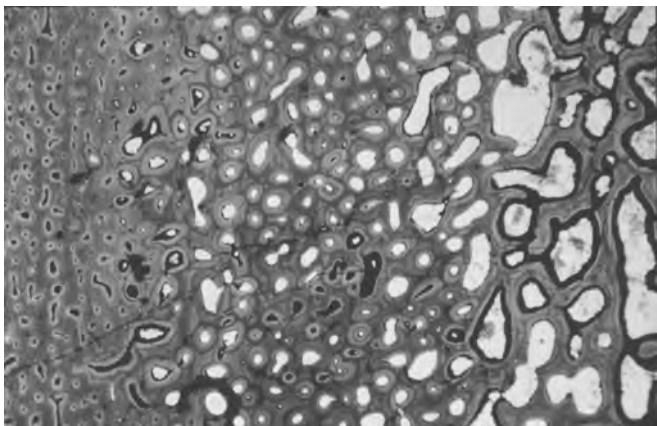
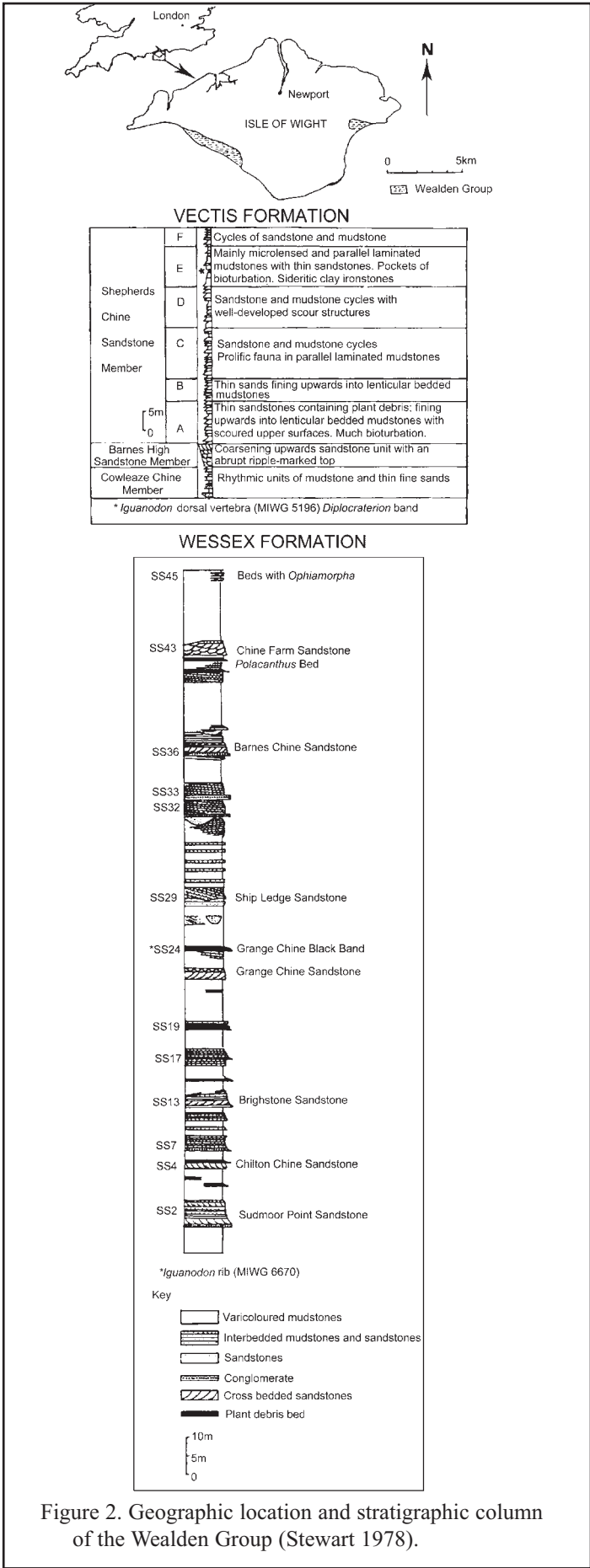


Figure 1. Section through a plesiosaur propodial showing the voids in which minerals are precipitated. The periosteal (outer) surface on which primary bone is deposited throughout life is off the frame to the left. The cortex, to the left of the frame, contains voids left by blood vessels. The transition zone occupies the central area of the frame and is where primary bone is constantly reworked into secondary bone; the circular voids previously containing blood vessels. To the right of the frame the inner cancellous zone, made up of secondary bone, has larger voids to keep the bone as light as possible which, in life, would have been full of marrow.

Bone consists of a framework of struts surrounding voids which in life would have been full of blood and marrow (Figure 1). When empty these provide ideal sites for the precipitation of authigenic minerals which are precipitated from the solutes in the



percolating groundwater. Layers of minerals are deposited in each void until the voids are filled; sometimes up to as many as 10 mineral phases can be deposited in a void 1mm in diameter. Once filled, the bone is physically very strong and can often withstand the pressures during burial without crushing.

The order of precipitation of the minerals, together with a knowledge of the individual precipitation requirements of each mineral, gives an insight into the solutes in the percolating groundwater. From this we can deduce the prevailing environmental conditions in terms of Eh and pH surrounding the bone at each stage.

Each bone can be read like a geological map and this paper will describe and compare two case studies and see what conclusions can be drawn.

The two bones are from the Wealden Group which outcrop in the Isle of Wight (Figure 2) and were kindly lent by the Museum of Isle of Wight Geology (MIWG). The Wealden Group consists of the Wessex Formation, mainly mudstones with sandstones and the occasional plant debris bed, with the Vectis Formation, mainly sandstones, on top.

Allen (1981) suggested a model for the deposition of the Wealden as a basin fed from rivers from three landmasses: Armorica to the south, Cornubia to the west and Londinia to the north. Although he showed a connection with the Tethys Sea it was not clear whether the basin contained fresh, brackish or marine water.

Wach and Ruffell (1990) carried out XRD analysis on the clay fraction from the Vectis Formation and proposed an outwash delta and lagoonal environment fed from the west which was prone to flooding but, again, there was no mention of the nature of the water.

The first case study is that of an *Iguanodon* late dorsal vertebra (MIWG 5196) (Figure 3), which came from the *Diplocraterion* band in the Shepherds Chine Sandstone Member of the Vectis Formation (Figure 2); this is unusually high in the formation for dinosaur bones to occur. The vertebra is 150mm from top to bottom; the space where the spinal cord passed through is visible; the ribs and neural spine have broken off and there are two cracks on the shoulder of the centrum. There is a large crack through the centre of the centrum and several smaller cracks through the cortex of the centrum.

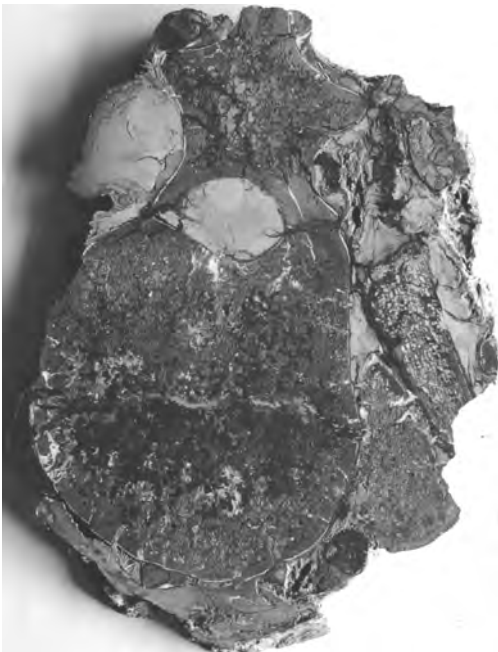


Figure 3. Section through an *Iguanodon* late dorsal vertebra MIWG 5196. Long axis 150mm.

The order of events is as follows:

The outer surface was bleached in oxic conditions and the organic content was consumed by bacteria.

The bone cracked whilst immersed in water and two muds of differing viscosity were sucked into the crack. This indicates that there was an oxic layer of grey mud in contact with the water overlying an anoxic black bottom mud.

The muds flowed into the crack and infiltrated the surrounding voids where they solidified, forming casts of the voids. The black mud pyritised (FeS_2).

A brecciation event followed cracking the bone trabeculae which were held in place by the mud casts.

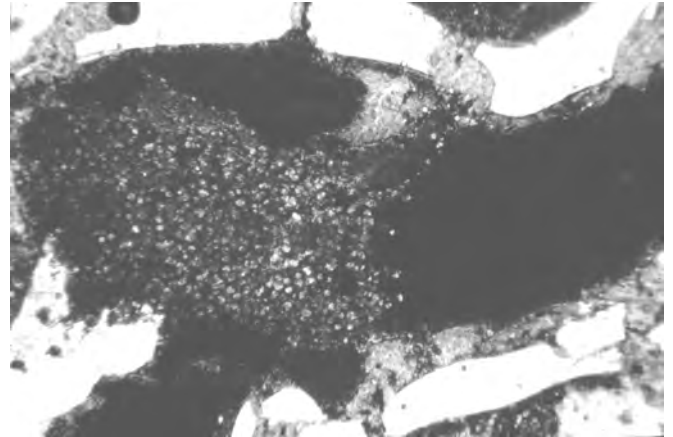


Figure 4. Siderite crystals formed within pyritised mud. MIWG 5196, stained section, frame width 2.3mm. ppl.

Siderite (FeCO_3) crystals then formed within the mud and in between cracks in the trabeculae (Figure 4). There are two sizes of siderite crystals small ones and larger ones which appear to be two phases of precipitation, the second phase nucleating on the first phase (but see note at the end of the paper).

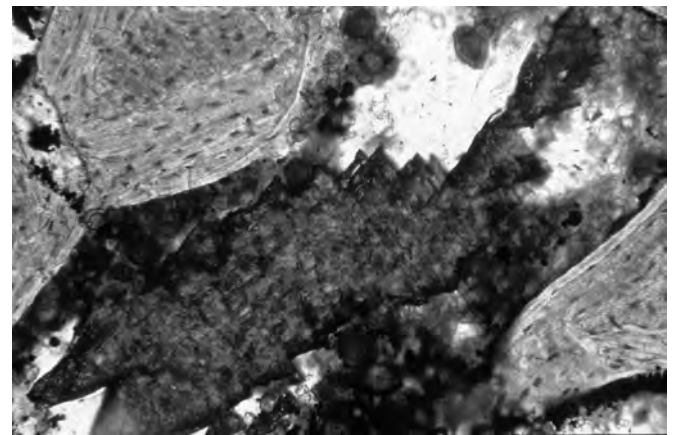


Figure 5. Sphalerite crystals. MIWG 5196, Width of frame 1.5mm. ppl.

Sphalerite (ZnS) came next (Figure 5) followed by ferroan calcite ($[\text{Fe,Ca}]\text{CO}_3$) and finally, the cracking of the cortex of the centrum and the precipitation of facicular-optic barite (BaSO_4) (back cover of the Journal bottom left).

Two ways have been developed to display this sequence: a diagenetic pathway plotted on a fence diagram (after Krumbein & Garrels (1952)) which defines the pH and Eh conditions required for the precipitation of various minerals and has been adapted to cover the minerals found within the vertebrate fossils studied (Figure 6), and the compilation of a Minstrat (Clarke 1997).

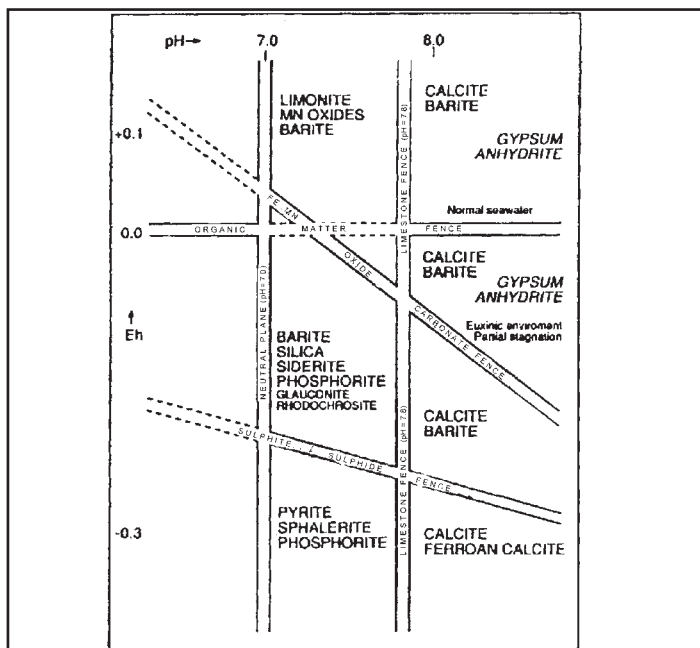


Figure 6. Fence diagram (after Krumbein & Garrels 1952).

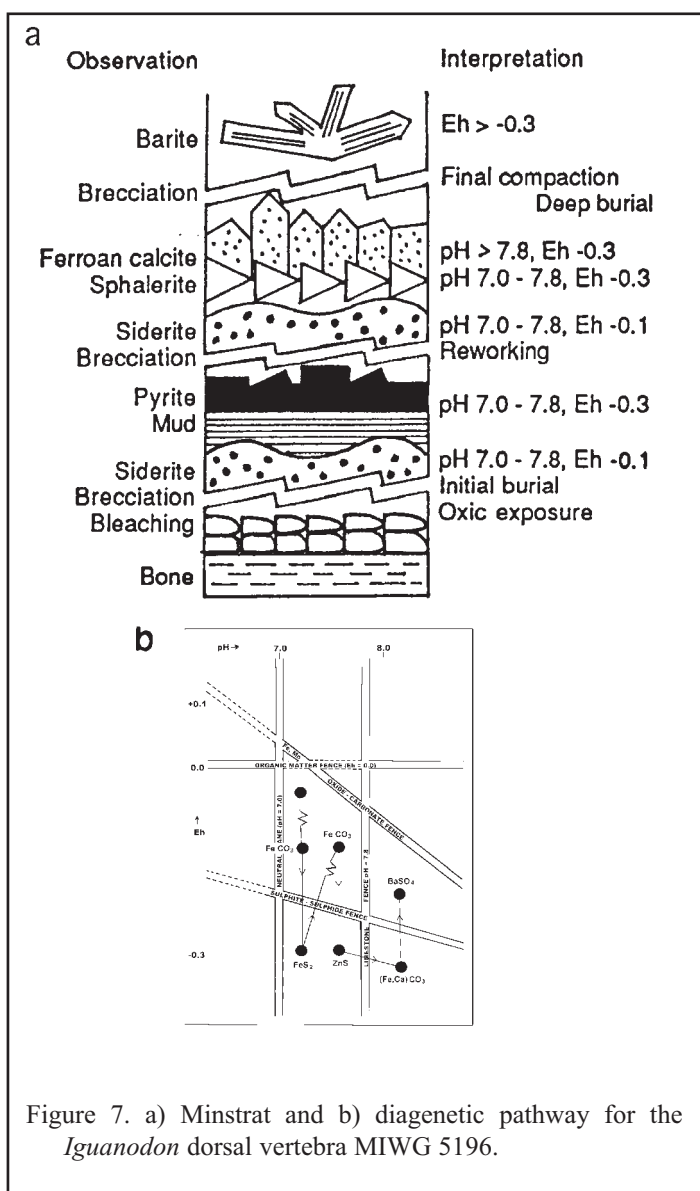


Figure 7. a) Minstrat and b) diagenetic pathway for the *Iguanodon* dorsal vertebra MIWG 5196.

The minerals and events occurring in the vertebra are plotted on the fence diagram in their order of precipitation and the pathway drawn (Figure 7a). The Minstrat is compiled by placing a pictorial representation of each mineral in a vertical column in the order of precipitation - a mineral stratigraphic column - in which brecciation events are also included. Observations and interpretations can be added thus giving a full history of the diagenesis of the bone (Figure 7b).

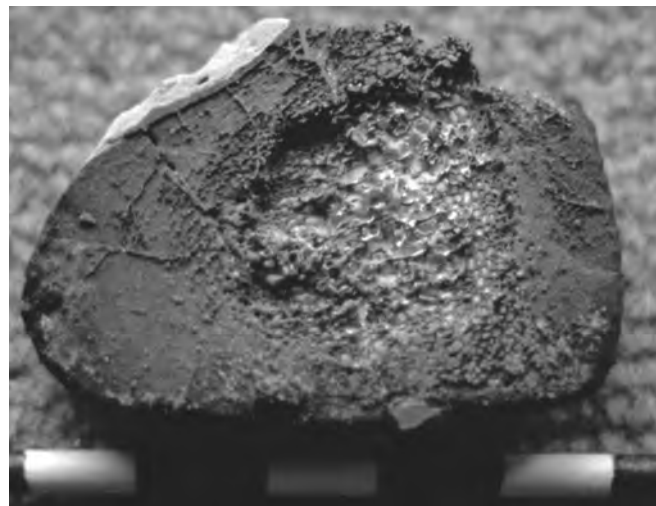


Figure 8. Heavily etched section through *Iguanodon* rib MIWG 6770. Scale in cms.

The second case study concerns an *Iguanodon* rib (MIWG 6770) (Figure 8) which came from the Grange Chine Black Band, a plant debris bed in the Wessex Formation (Figure 2).

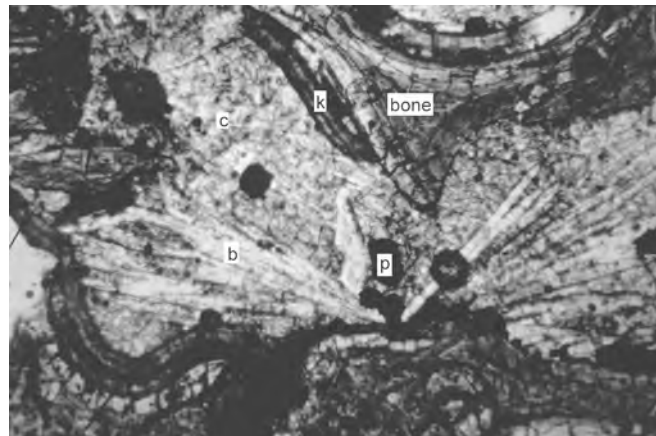


Figure 9. Thin section of rib MIWG 6770. b-bladed barite; c-calcite; k-kutnohorite; p-pyrite. Frame width 1.5mm. ppl.

A thin section of the rib (Figure 9 and back cover of Journal) reveals siderite ($[\text{Fe,Ca}]\text{CO}_3$) (not shown), barite (BaSO_3), pyrite (FeS_2), calcite (CaCO_3) and an unusual feature - a uniform thickness film composed of several layers which appears to have flowed over some of the bone trabeculae. This layer is a lithified bacterial mucilage preserved as kutnohorite ($[\text{Ca,Mn}]\text{CO}_3$) and this was the first time it had been identified. When examined with a scanning electron microscope the crystallisation of the film was revealed (Figure 10); clearly the viscous substance had flowed over the bone and just stopped. Bacteria cannot live directly in air or water so they create a slime (mucilage) in which they live. This mucilage had infiltrated through two cracks in the bone and had migrated through the interconnecting voids. The interesting property of this mucilage, as far as diagenesis is concerned, is that this

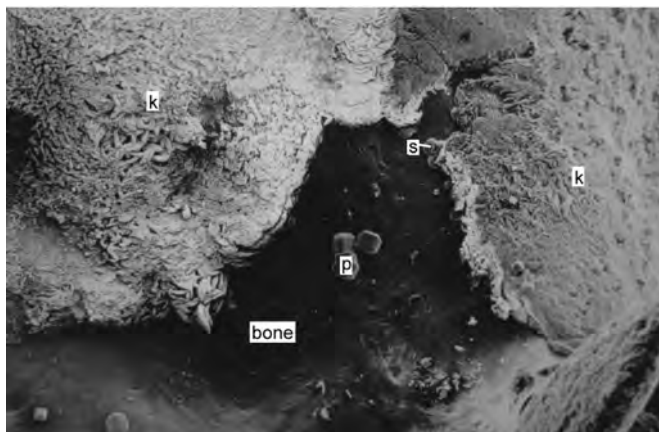


Figure 10. SEM image of MIWG 6770 showing two flows of mucilage which stopped before converging. k-kutnohorite; p-pyrite; s-siderite. Frame width 2.3mm.

mucilage contains manganese; only freshwater bacteria use manganese so the inference is that this bone was residing in a freshwater environment soon after the removal of soft tissue.

The presence of this freshwater bacteria confirms Wach & Ruffell's model of a mostly freshwater environment of overbank and lacustrine deposits.

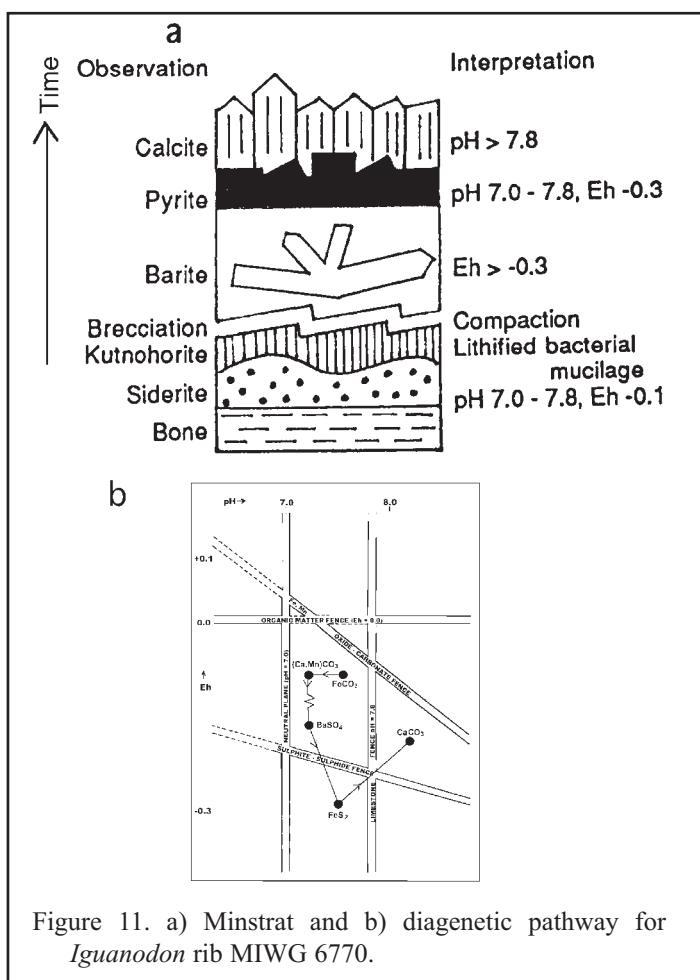


Figure 11. a) Minstrat and b) diagenetic pathway for *Iguanodon* rib MIWG 6770.

If we compare the Minstrat of the rib (Figure 11b) with that of the vertebra described earlier (Figure 7b), it is apparent that the rib has a far simpler history; there are far less symbols in the column. If we compare the diagenetic pathway of the rib (Figure 11a) with that of the vertebra (Figure 7a) it can be seen that the rib describes one cycle whereas the vertebra describes two cycles.

The inference is that the rib was buried and remained so until exhumed recently, whereas the vertebra was buried, acquired some minerals, was exhumed, reburied and started the cycle again. Apart from the vertebra occurring high in the sequence there is no indication of a discontinuity or reworking event in the sediments, so this bone has revealed an event hitherto unrecognised.

So what we have here is a method of determining the prevailing palaeoconditions during the taphonomy and early diagenesis of individual fossils, from which we can deduce the conditions prevailing within the early diagenesis of the sediments.

These are just 2 of 35 samples taken from different strata throughout the sequence. It was hoped that each horizon would have a distinctive signature, but that was not the case. However, specimens from Sandown have experienced much harsher conditions than those from Brighstone Bay which indicates differences in the sediments and solutes coming from the landmasses of Cornubia and Armorica.

Much more detailed research is still needed.

Acknowledgements

Thanks go to Steve Hutt of the Isle of Wight Museum for the loan of the specimens; to Keith Simmonds for originally supplying the rib; to Dave Martill (formerly of the OU, now of Portsmouth University) who planted the seed of the Minstrat idea and to Portsmouth University for the use of their scanning electron microscope.

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NB. After my talk at the Symposium Professor Alan Dyer, University of Salford, informed me that two sizes of siderite crystals did not necessarily indicate two phases of precipitation. Apparently it is well documented that one precipitation event can result in multiphase crystals (see, for example, Thompson 1992). I have noted this for the future. I shall remove the first siderite event from both the Minstrat and the diagenetic pathway for the vertebra, but it does not change the overall argument and result.

Fossil forests of the polar regions: heralds of global climate change

Dr Jane Francis, School of Earth Sciences, University of Leeds

It is now well known from fossil evidence that forests once flourished in the polar regions before our present Ice Age set in. Although the Arctic and Antarctica that we know today are covered by ice sheets and glaciers, this was not the case for most of Earth history. Before about 2Ma in the Arctic and 38Ma in Antarctica, when the ice sheets of the present glaciation became established in each region respectively, these regions saw forest vegetation well into the polar circles.

These forests, which lived in higher latitudes than forests are found today, represent an ecological niche that has no modern living counterpart. We can only understand how such unique ecosystems worked by fully exploring the evidence left behind in rocks and fossils. These forests are also important recorders of climate information. It is the high latitude regions that record the first signs of climate change, both now and in the past. The record stored within fossil plants is thus a crucial signal for understanding the beginnings of climate change that subsequently affect the whole Earth.

This paper presents a brief description of some Cretaceous and Tertiary forests and climates in the Arctic and Antarctica.

Antarctica

The Antarctic continent has, in fact, a longer history of forest cover than it does of ice. The continent was covered with extensive ice sheets during the Late Palaeozoic glaciation that covered Gondwana (Late Carboniferous in Antarctica) but from the Permian until the late Eocene there is a good record of fossil



Figure 1. Cretaceous and Tertiary rock sequences on Vega Island, Antarctic Peninsula. The lower part of the sequence is composed of marine siltstones, deposited on a shallow marine shelf during the Late Cretaceous. These beds contain both marine fossils and plant fossils that were washed in from the adjacent Cretaceous land. Geologists for scale.



Figure 2. Fossil wood, permineralised by calcite, preserved within marine carbonate nodules in Late Cretaceous sediments, James Ross Island.

plants, especially of *in situ* tree stumps, that indicates forests in Antarctica throughout that time. For example, there are Permian and Triassic fossil forests in the Transantarctic Mountains, and Jurassic to Tertiary floras in the Antarctic Peninsula region.

The last major greenhouse climate phase was during the Mesozoic. At this time forests clothed the volcanic terrain that now forms the Antarctic Peninsula region, part of a subduction-related arc. In particular, during the Late Cretaceous and Palaeogene forests grew on the flanks of these active volcanoes, even though the area was situated at about 65°S, the same latitude as it is today. Tree trunks and branches, leaves, flowers, seeds and pollen were washed into adjacent seas to the east and subsequently buried in shallow marine sediments, now exposed on James Ross, Vega and Seymour islands (Figure 1). Wood was permineralised (Figure 2) and leaves preserved as impressions in carbonate nodules and now provide a record of forest composition and the climates at that time.

Studies of leaves, wood and pollen from these sediments indicate that the forests were composed of many plant types that are now characteristic of modern southern vegetation, particularly from South America and Australasia. Conifers include the Araucariaceae (relatives of modern Monkey Puzzle) and the podocarps. Flowering plants (angiosperms) include relatives of modern families such as Winteraceae and Nothofagaceae (southern beech). During the Cretaceous some types now typical of subtropical climates, such as Lauraceae and Sterculiaceae (Figure 3), were found in Antarctica, suggesting much warmer climates than present.

The climates under which these plants grew can also be deduced from analysis of leaf architecture, based on our understanding of the relationship of modern leaves with present climates. For example, leaves with smooth margins are known to inhabit mostly warm climates today, whereas those with toothed margins live in cooler climates. When these analyses, such as leaf margin analysis (see OU book 'Evolving Life and the Earth' course book for S269 Earth and Life) are applied to Antarctic floras, mean annual temperatures of about 20°C are estimated for mid Late

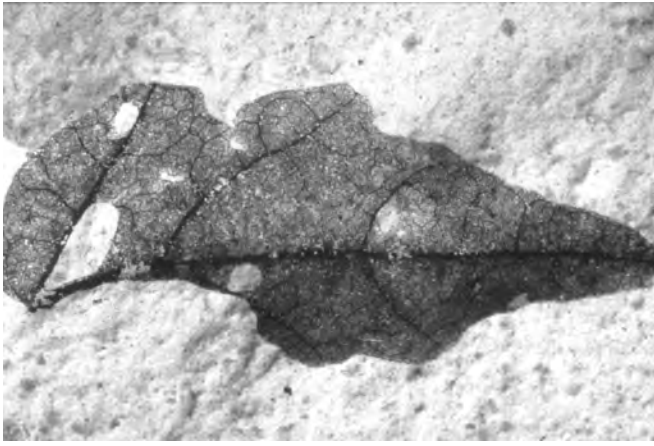


Figure 3. Fossil leaf of Late Cretaceous age from James Ross Island, Antarctica. This leaf is probably representative of the modern sub-tropical family Sterculiaceae (identified by P. Hayes, 2000, PhD thesis, University of Leeds). The round holes in the leaf are probably due to insect damage. Leaf approx 3cm in length.

Cretaceous times (Coniacian) (Hayes 2000, PhD thesis University of Leeds) and 13°C for the Palaeocene (Tosolini pers comm) – temperatures considerably higher than the freezing temperatures of this region today, and too warm for the existence of ice.

We can see a change in the composition of floras through the Tertiary, as the warmth-loving plant types give way to vegetation dominated by southern beech that can tolerate cool temperate climates. This mirrors the cooling climate as ice built up on Antarctica from about the latest Eocene at 38Ma. The last trees in Antarctica are found as mummified fossils of southern beech, encased in Pliocene glacial sediments high in the Transantarctic Mountains. Mats of leaves and small twigs of wood show that these plants were small dwarf shrubs that clung close to the ground, trying to survive the harsh tundra environment. The ice sheets advanced once more and the last remnants of the great Antarctic forests were finally wiped out.

The Arctic

Fossil floras are also preserved in Cretaceous and Tertiary strata in the Arctic, evidence for greenhouse warmth in the northern



Figure 4. Fossilised leaf litter from Eocene forests, Axel Heiberg island, Canadian Arctic. Most of the foliage consists of the delicate feathery leaves of dawn redwood. A cone of dawn redwood is also visible in the centre of the picture (about 1cm in diameter)

regions (see S269 course book). One particularly famous forest occurs in the Canadian Arctic islands, at latitudes of about 80°N today. During the Eocene this region was also situated at about 80°N but it was covered with rich forest vegetation even at such high latitudes because the climate was so warm.

On the islands of Axel Heiberg and Ellesmere in the Canadian Arctic layer upon layer of fossil forests are preserved on hill sides. Thick layers (up to 1 metre) of delicate leaves, twigs, cones, seeds and wood are preserved as dark layers and represent the fossilised remains of forest floor litter (Figure 4). The fossil material is unusually preserved; it is simply mummified and appears compressed, dried and blackened. The wood can easily be cut with a saw and burnt, even though it is over 40 million years old. In some regions where the same rock strata have undergone tectonic deformation, the tree stumps have been permineralised by carbonate minerals and remain as upright stumps within the fossilised leaf litter (Figure 5).



Figure 5. Permineralised tree stumps exposed on a level of a forest floor, Strathcona Fiord, Ellesmere Island. The spacing of the tree stumps indicates that the forests were quite dense.

These forests were once growing on flood plains and swampy areas near large rivers that flowed across this Arctic region. Switches in river channels and flooding events buried the forest floors rapidly with layers of mud and sand, preserving them intact, layer upon layer.

The Arctic forests have a completely different floral composition to those from the Antarctic. The forests were dominated by the conifer *Metasequoia* (dawn redwood), a tree that was first discovered as fossil leaves from Northern Hemisphere Tertiary sites but then discovered to be still living today in China. *Metasequoia* has fine feathery foliage and flared buttress roots very similar to modern swamp cypresses that live today in the Florida Everglades, a good adaptation for living in swampy conditions. Other fossil plants found in these forests include the scale-leaved conifer *Glyptostrobus*, several types of pine, spruce, larch and flowering trees such as alder, hickory, and *Cercidiphyllum* (katsur).

Fossil bones have been found in adjacent strata and show that animals lived in these forests too. They include turtles and tortoises, primitive horses, crocodiles, a hippo-like creature called *Coryphodon* and even flying lemurs (see Figure 6). This polar paradise presents a very different picture to the harsh tundra environment of the Arctic today.



Figure 6. Reconstruction of the Eocene fossil forests of the Arctic, by Cliff Morrow, Carnegie Museum of Natural History, USA.

How did these forests survive at such high latitudes?

There are two factors that would have had important influences on forest survival in the polar regions – temperature and light.

It is clear from evidence from fossil plants that temperatures never dropped below freezing for extended periods, because many of the plants could not have survived severely cold winters. There are also no signs of frost damage in the fossil tree rings that would have been a signal of late spring or early autumnal frosts. In addition, the presence of crocodiles at high latitudes in the Tertiary Arctic forests has often been given as evidence for lack of cold winters at the poles. Nevertheless, the winter temperatures must have been rather cool in order to force the plants into hibernation during the dark winters so that they did not continue to respire during the dark and use up their food stores.

These forests had to cope with an unusual light regime, that of several months of continuous summer sunlight followed by winters with months of darkness. The plants clearly coped well with this, as there is no indication that they suffered in any way. They probably made full use of the long days of summer sunlight but became dormant during the dark winters, and may well have shed their leaves as a mechanism for survival – many of the fossil plants are deciduous types today, especially those that lived in the Arctic.

With the continuation of global warming today plant species are migrating slowly towards the high latitudes once again. It is clear that, so long as barriers such as wide oceans can be breached, forests have the ability to grow once more in the polar regions.

Book review

The Archaeology of Geological Catastrophes by W J McGuire, D R Griffiths, P L Hancock & I S Stewart (eds), 2000, **The Geological Society, London** 417pp, £79 (hardback) ISBN 1862390622.

The Archaeology of Geological Catastrophes is a book that combines two of my favourite loves: geology and archaeology. The book contains a collection of 28 diverse papers discussing how geological investigation assists in the archaeological identification and cultural significance of large-scale geological events, mainly earthquakes and volcanic eruptions. However, this is shown as a two-way street.

Archaeology provides the geologist with one more tool to decipher the present is the key to the past. By investigating the historical archives and geological features found in archaeologically significant sites, the geologist may be able to reduce the present hazards posed by earthquakes and vulcanism. By learning to recognise the signs of geological catastrophes, the archaeologist may find the missing piece, which better explains cultural development or demise of a given region. For example, the 464 BC earthquake at Sparta, Greece, triggered a major change in the political climate in the Peloponnese. By examining archaeological research, earthquake geologists have been able to estimate the earthquake energy released on a major fault that has since that time been seismically quiescent.

This book is definitively a book to dip into. The broad spectrum of papers provides us with not only the evidence of the destructive powers of geo-hazards, but the benefits to cultures as well. Fertile soils and materials for tools, building and sculpture are products our ancestors used to build the civilisations we now read about. Historical records provide a useful point of reference, but we are also warned that this must be used with caution.

The cross-disciplinary nature of this book and the papers shows the co-operation that is needed to provide key answers to the past and at the same time assist in the prevention of cultural disasters in the future.

Papers address the human reactions to both local and regional events, (e.g. the Icelandic eruptive activity on the agricultural demise in the Scottish Highlands).

Numerous papers in the book present interpretations of the Bronze Age eruption of Thera (Santorini, Greece) and its regional impact on the Minoan culture. In addition, case studies from Italy, Germany, the Canary Islands, the Cape Verde islands, Yemen and Mexico illustrate the global nature of geological hazards. Whatever your personal interest, you are likely to find a paper or two you'll enjoy. I personally found the paper on the Minoan marine ware pottery extremely fascinating. The paper discussed how the change in the marine environment in the Aegean was evidenced by the change in motifs found on Minoan vessels. And to see a geological slant to the Olmec basaltic sculptures was most refreshing to me.

While the majority of papers presented their theories and data in a form I felt comfortable to assimilate, there were some areas I was completely at a loss to understand. In general, because of my educational background, I found the interdisciplinary nature of this book a fascinating and excellent read. At a price of £79 (£35 for members), this is most likely not a book that will grace many a geologist/archaeologist's shelf. I would, however, recommend using it to supplement any research one might be doing be it geological, archaeological or historical.

Diane M. Culpin, BA Hons Continuing ES Student

How bad is the fossil record?

Professor Mike Benton, Dept of Earth Sciences, University of Bristol

My topic is the quality of the fossil record; a topic that palaeontologists keep coming back to time and time again. This talk will try to develop the theme that we do have to keep asking this question, because we cannot simply assume that the rock record is adequate to tell the story of the history of life. We have to keep testing and defending and looking at it again and again.

There are two aspects of completeness that need to be considered.

One aspect of completeness, relative completeness, is how much we know of the fossil record as it is in the rocks. In other words, how near are we to finding all the different fossils that are in the rocks? The other aspect, which we could call absolute completeness, is how much does that fossil record actually represent the true shape of the history of life? In other words does it take into account those organisms that have never been fossilised? It should be possible to find ways of looking at the first part because, if fossils are in the rocks, the more they are collected, the more will be found and the more the record can be quantified.

To assess what has not been fossilised might seem to be rather difficult; ultimately it is, but maybe there are ways to try to discern some part of it. Why is it important? It is important because the fossil record means more than the fossils in the rock that so fascinate palaeontologists and fossil collectors; potentially, it is the record of the history of life and, right from the times of Lyell and Darwin, people have recognised this important fact. What we decide, and subsequently try to convince the rest of the world, will impact on non-earth-scientists tremendously. This talk will try to show that this theme keeps recycling and recycling, most recently in a huge enterprise to reconstruct the history of life, or the Tree of Life Project as it has been called, based on molecules of extant organisms. Therefore there is a potential tension between these two approaches, but also a potential marriage between them, so we will have a brief look at that as well.

Life today is hugely diverse, both on land, in the form of animals and plants, and in the sea. That vast diversity, that almost excess diversity of life, is a whole theme in itself which I will not go into. A question that obviously motivated Darwin in his earliest days as he went round the world was to estimate how many species there are. To understand the history of that diversity we can look at it in two different ways. One way is phylogeny: i.e. an evolutionary tree.

The first attempt in Europe to construct an evolutionary tree was illustrated by a very famous diagram by Haeckel (1866) in which he showed it just like a tree.

We would normally show the phylogeny of life with a stratigraphical range chart with ancient times on the left and present day to the right. It looks like a pattern of inter-relationships with constant addition of new groups without major groups going extinct.

Another way to look at the diversity of life in the historical sense is simply to produce a diversity graph showing the change in the diversity of life through time. This type of diagram is derived from the summation of lots of range charts showing the distribution in time of individual families, of genera, or of species. These

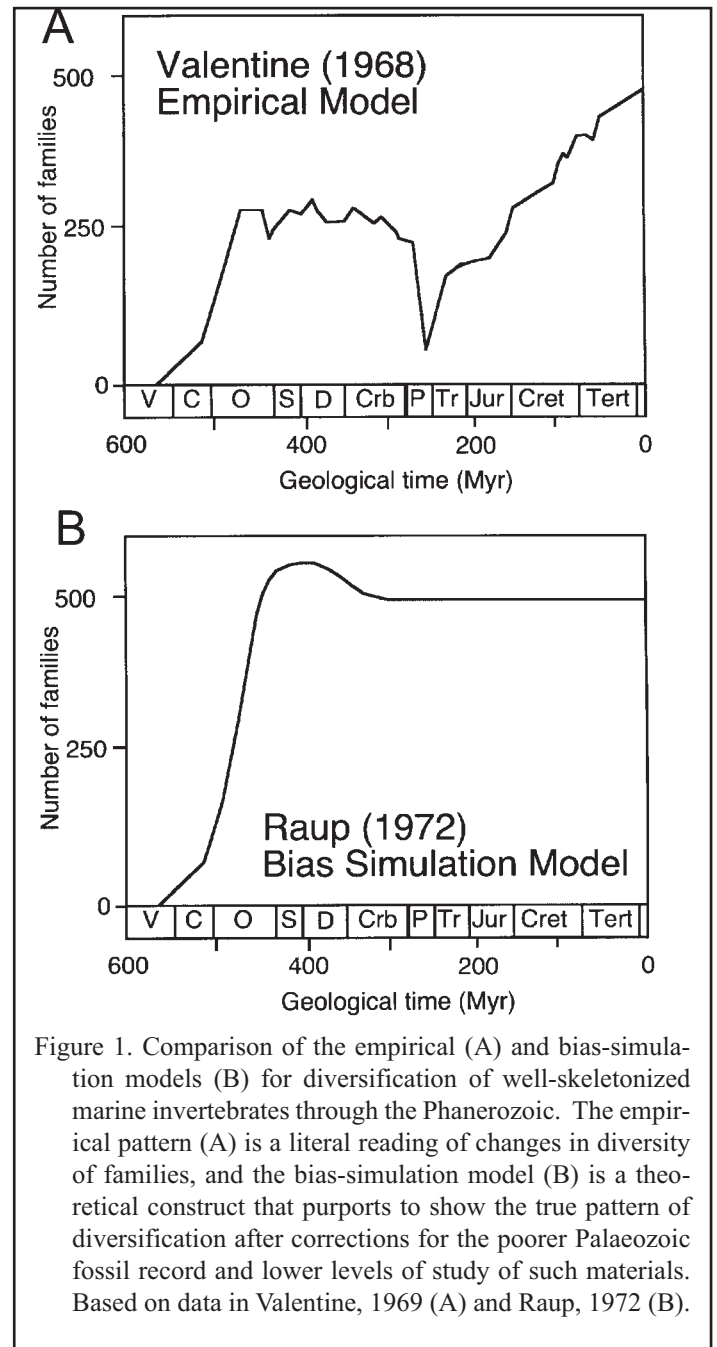


Figure 1. Comparison of the empirical (A) and bias-simulation models (B) for diversification of well-skeletonized marine invertebrates through the Phanerozoic. The empirical pattern (A) is a literal reading of changes in diversity of families, and the bias-simulation model (B) is a theoretical construct that purports to show the true pattern of diversification after corrections for the poorer Palaeozoic fossil record and lower levels of study of such materials. Based on data in Valentine, 1969 (A) and Raup, 1972 (B).

plots can be studied in detail to look at possible defining factors and the different rates of extinction and origination can be calculated.

Empirical or Bias Simulation Models

The debate about the reality of the meaning of those sorts of pattern was begun in the 1970s by Jim Valentine, a distinguished American palaeontologist, who presented the first serious attempt to add up all of the known fossil record. He tried to avoid the problem of representing what is in the rock by simply looking at well-skeletonised marine invertebrates, things like brachiopods, molluscs, arthropods, echinoderms and so on (Figure 1a). His argument was that because we believe for qualitative reasons that the fossil records of these groups are very good, we can try an

empirical plot of their relative diversities through time. He said that he had assumed that less well-preserved groups like jellyfish and worms and the rest, would presumably follow a similar pattern. In the 1960s he was one of the few to see some of the aspects of the pattern: the rapid rise in the Cambrian, a levelling off in the Palaeozoic, a drop at the end of the Permian and the continuing rise toward the present.

Another equally distinguished American palaeontologist, David Raup, countered this with a very important paper in *Science* in 1972, when he presented the so-called Bias Simulation Model (Figure 1b) in which he argued that all that Valentine had plotted was our knowledge of the fossils as preserved in the available rock. He said that the empirical pattern was not very close to reality; it is really controlled by the volume of rock. We will come back to that later.

Raup suggested, for theoretical ecological reasons, that his Bias Simulation Model is more likely as it shows a rapid rise during the Cambrian explosion, an overshoot, then a levelling off to a kind of ecological equilibrium. The theoretical reasoning there will be familiar to anybody who has studied basic ecology: the Lotka-Volterra models, Poisson distributions etc. These are the kind of results obtained in simple competition experiments in petri dishes. Raup believed that that was the way things were.

There is a grey area on his graph which results from a variety of sources of error. Clearly, the further back in time you go the less surviving volume of sedimentary rock of any age is available: the area of calibrated Cambrian rocks exposed is less than for the Cretaceous because younger rocks are lying on top and the older rocks are unavailable. This leads to several human aspects which appear to be true. It is the case that the number of people per million years of time working on Cambrian and Ordovician fossils are far fewer than those working, for example, on Pleistocene or Neogene fossils. There is a correlation there: the more palaeontologists who study any particular time interval or group, the more detail is observed and the more species discovered.

If you are studying some group or class of animals that have living relatives, you have a better way of knowing how to subdivide the species. So the species of Tertiary mammals or of Tertiary angiosperms are much more precisely divided according to comparisons with living forms than trilobites which have no close relatives. These would tend to inflate the part of the record that approaches the present day and reduce that part of the record that is more ancient.

Now that was quite a challenge, but it was thought to have been resolved in 1981 in a paper by Jack Sepkoski and other authors, including both Raup and Valentine; it was a sort of political statement. In that short paper in *Nature* they said that the fossil record, the empirical pattern, broadly speaking, is accurate. So Valentine's viewpoint was accepted.

In their paper these authors compared five independently compiled sets of data on the history of life, at different taxonomic levels, species, genera and families which had been prepared by different people. It was argued that because the data sets are independently compiled and because they all showed the same pattern, that pattern ought to be real. But the one thing that was glossed over at the time (and has been pointed out several times since) was that these five data sets may have been independently

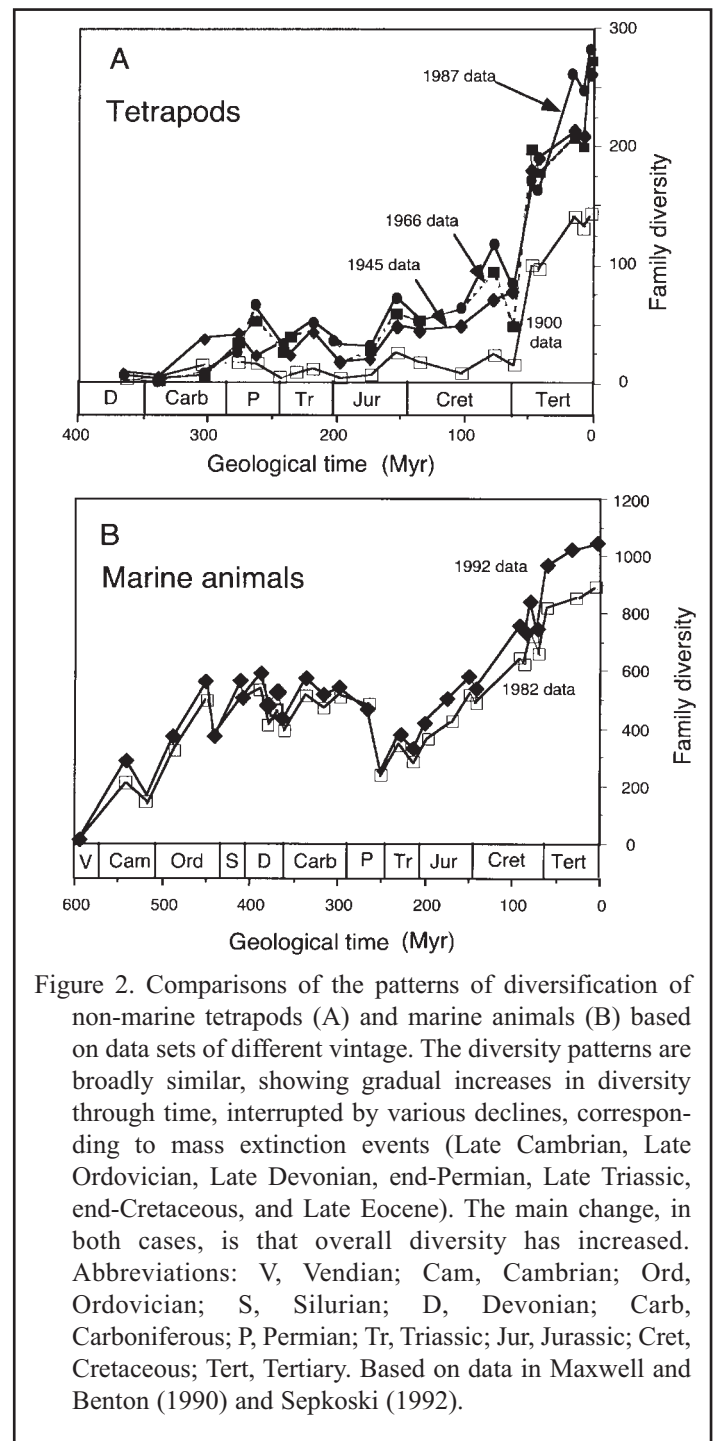


Figure 2. Comparisons of the patterns of diversification of non-marine tetrapods (A) and marine animals (B) based on data sets of different vintage. The diversity patterns are broadly similar, showing gradual increases in diversity through time, interrupted by various declines, corresponding to mass extinction events (Late Cambrian, Late Ordovician, Late Devonian, end-Permian, Late Triassic, end-Cretaceous, and Late Eocene). The main change, in both cases, is that overall diversity has increased. Abbreviations: V, Vendian; Cam, Cambrian; Ord, Ordovician; S, Silurian; D, Devonian; Carb, Carboniferous; P, Permian; Tr, Triassic; Jur, Jurassic; Cret, Cretaceous; Tert, Tertiary. Based on data in Maxwell and Benton (1990) and Sepkoski (1992).

compiled but they are not in themselves independent, because they are all based on the same fossil record. So the key point that Raup had made had not been answered. However, palaeontologists kept quiet about that during the 1980s and 1990s because of the opportunity to use the fossil record produced in the classic work by Raup, Sepkoski and others who looked at the diversification of marine invertebrates, plants and vertebrates and at the patterns of mass extinctions, the timings and the periodicity. All this work was based on the conclusion that was made in 1981, that it is all right to accept the reasoning behind the models.

I tend to support the work of Raup and Sepkoski and their view that their reasoning is acceptable. However, there are suggestive findings that tend to support the view that the method is only valid to a certain extent; there is a caveat: even though, in the course of

the last hundred years, our knowledge of the fossil record has improved enormously, the patterns that are derived from it have not changed much.

In 1990, Des Maxwell, a student of mine, published a graph of diversity through time for terrestrial tetrapods. He looked at a number of compilation books and at major texts published over the last hundred years from 1900 through to 1987. His graph (Figure 2a) shows that the number of families of tetrapods has doubled throughout. Additionally, the number of new dinosaurs and other genera that are being announced all the time, clearly gives a net increase in the diversity of animals with the passage of time. Interestingly, there has been no bias in the parts of the record that have increased; the overall shape has not changed much between 1900 and 1987. I am sure if there was an additional survey to the year 2000 it would not be much different. This tends to suggest that the detail of what we put in to these kinds of calculations does not matter too much. Somebody looking at this question in 1900, with so much less information, would still have come up with the same conclusions.

Jack Sepkoski did the same thing (Figure 2b) on a more limited timescale, from 1982-92, from the Vendian to the present day and he argued strongly that the only thing to change was that the extinction events had been sharpened up.

That has been confirmed again in a very detailed study by Jonathan Adrain (2001) published last year in *Science*, where he looked at a very small part of the Sepkoski data-set on genera, so he was focusing down on a lot of detail. Sepkoski had compiled this vast data-set (which is unpublished) of thirty thousand or more genera of marine fossils through time. People have been using that ever since and yet everybody knows that the data-set is riddled with error (Sepkoski himself was the first to admit it; he was just compiling it as quickly as he could because to get thirty or forty thousand records by one person means that corners have to be cut). Did that matter? The interesting thing was that Adrain and colleagues went through his record of trilobites through the Ordovician and the Silurian and they found that the levels of error were quite high, up to 30-40% for some time intervals. It would be expected that 40% error in some time intervals would be quite catastrophic but, comparison of the two records shows that there is no difference. So those two sets of studies are quite helpful in that they suggest that at least, for the first part of completeness, - the business of do we know pretty well what there is there in the rocks? the answer is 'yes' Even though the knowledge may be rather incomplete that does not matter for this kind of broad-scale study. But this does not tackle the deeper question of the quality of the record.

The molecular challenge

Two challenges have come recently; the first from molecular studies.

You all know the gist of how phylogenies can be derived from molecular data by comparing sequences of proteins or nucleic acids. The theory behind it, the molecular clock, is fairly accepted in its broad sense. It is very commonsensical, the view that if there are two organisms which are very closely related, analogous proteins or analogous segments of nucleic acids will themselves be very similar. If those two organisms are very distantly related, those segments of molecular structure would be very different. It can be calibrated pretty well: the amount of difference is roughly proportional to time since splitting.

Cladistic trees can be drawn looking entirely at the living representatives which is a very exciting proposition. A picture of the history of life can be drawn simply by looking at the fossils whilst the molecular biologist can draw up a similar diagram using only the living organisms. It is independent and there are not many areas of study to have such divergent or different sets of data that can be compared.

The molecular studies of the evolution of animal phyla, from sponges across to vertebrates, suggest that, although the fossil record of these may be sparse to Vendian times (600Ma) and shows the famous Cambrian explosion (550Ma), the molecular evidence largely seems to suggest that the animal groups began to diverge something like 1200Ma ago: twice as old!

What the molecular analysts are saying is that the first half of the fossil record of the animal groups is hidden from palaeontologists, and maybe always will be hidden. But we have the Ediacaran fauna to add to that; there may be chance discoveries but it seems unlikely. If that is true that is quite a challenge; it is suggesting that although we know the Phanerozoic part, we may never know the pre-Phanerozoic and hence that the fossil record is incomplete in that regard.

The second challenge concerns the radiation of modern mammal and bird groups such as whales, bats, primates, owls, birds of prey, penguins etc. The fossil record of these groups is almost entirely post-Cretaceous. Yet the molecular evidence has suggested that the origins of these groups were dated well down into the Lower Cretaceous. It suggests that *Iguanodon* were wandering about side by side with penguins, owls, camels and monkeys. If that claim is correct, that the molecular data is giving much older points of origin, then the fossil evidence for it is lacking. Why do we not find these fossils? There are all sorts of ways of saying why we do not find them but not finding them is not evidence that they are not there.

The rock volume challenge

The second challenge is the Raup argument again: the suggestion that the fossil record is almost entirely dependent on the vagaries of geology.

Andrew Smith (2001) from the Natural History Museum published a paper which contained a diagram which suggested different measures of biotic diversity through time. In it he shows a measure of percent flooding, measures of rock volume and other parameters (Figure 3). He did some very detailed statistical studies which seemed to suggest that all sorts of detailed ups and downs in the curves in the history of life (including even the K-T event) could be related to specific, transgressive and regressive episodes. He was suggesting that a large part of the diversification curve of our picture of the history of life is controlled simply by large-scale sedimentary events.

Shanan Peters and Mike Foote (2001, 2002), published two papers in which they went further. They suggested that all the patterns of diversification were almost entirely controlled by rock volume. They are suggesting very precisely what Raup had hinted at in 1972: that all the fluctuations in the graph are based on the volume of rocks available: the more rock there is, the more fossils will be found. It is extraordinary but maybe it can explain certain blips. There is an apparent extinction event at the Jurassic-Cretaceous boundary, for example, that is almost certainly an arte-

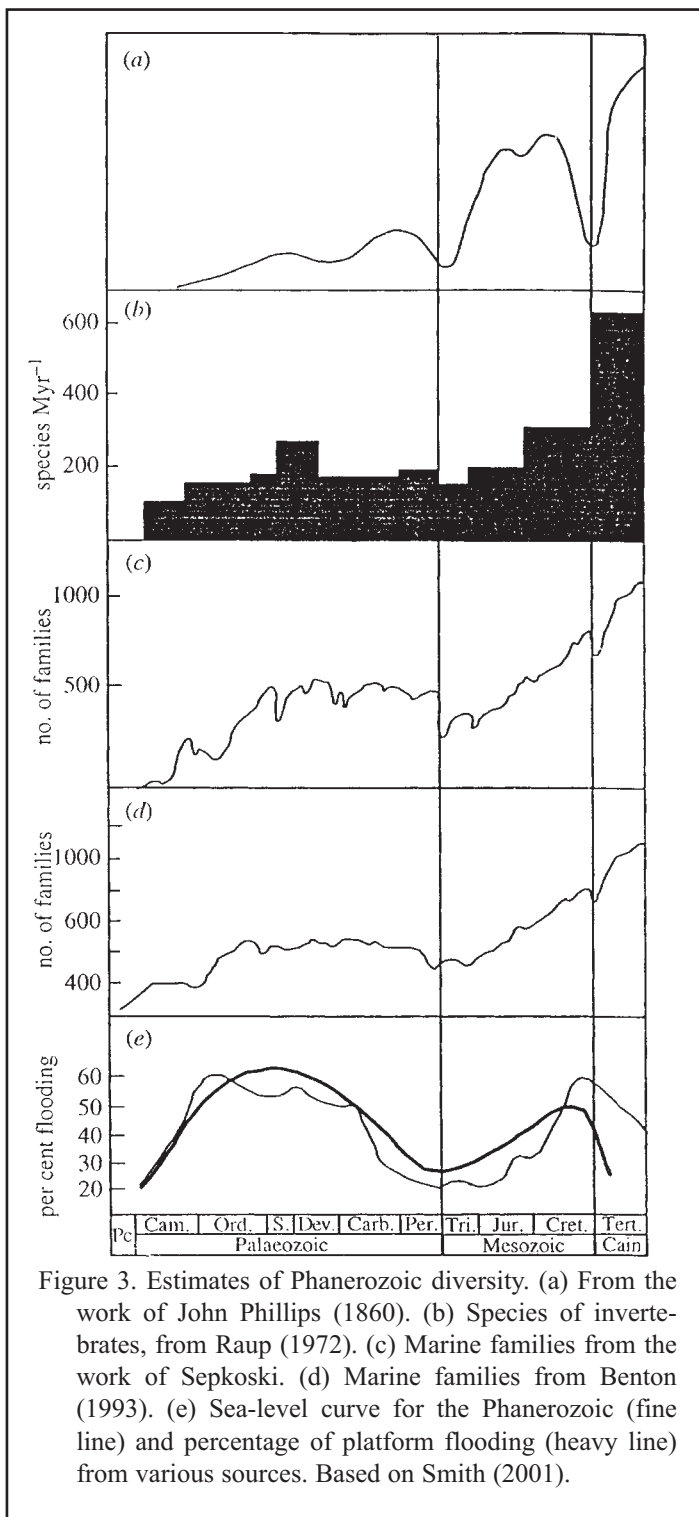


Figure 3. Estimates of Phanerozoic diversity. (a) From the work of John Phillips (1860). (b) Species of invertebrates, from Raup (1972). (c) Marine families from the work of Sepkoski. (d) Marine families from Benton (1993). (e) Sea-level curve for the Phanerozoic (fine line) and percentage of platform flooding (heavy line) from various sources. Based on Smith (2001).

fact of the rocks and the changes of habitats. But if the method removes the K-T event (as their method does) then I think their method is too crude. I think they would have to admit that there are certain major extinction events and if their method of statistical corrections removes these extraordinary events then it needs looking at again.

Is the fossil record hopeless?

Nonetheless, there are two challenges there, the molecular challenge and the rock volume challenge. If either, or both of them, are correct then it is saying almost the unthinkable - that the fossil record has got very little to tell us about the history of life. That would be an extraordinary circumstance if it were true. I do not believe it is.

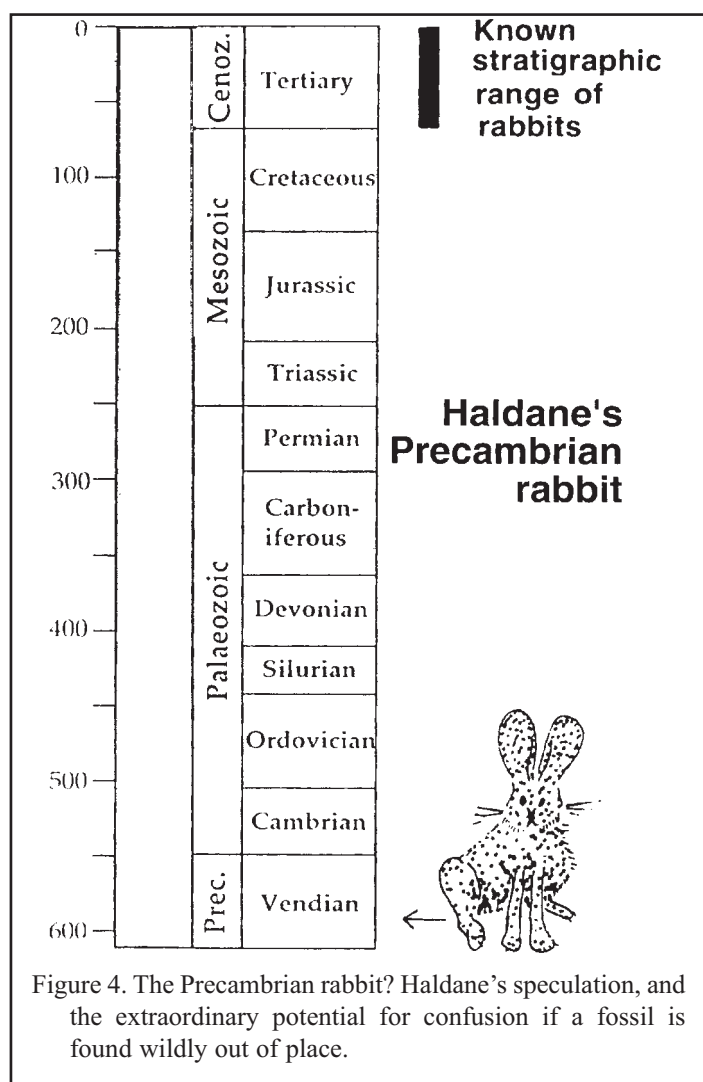
We are aware that certain kinds of fossil groups are extremely well-preserved: archaeocyathids, the trilobites from the Cambrian, ancient but rather well-known because of the hard parts, and certain vertebrates, such as dinosaurs, are exceptionally well known because of the bones. However, one does recall the existence of fossil lagerstätten and exceptionally preserved organisms like *Archaeopteryx*.

I remember when I was a boy learning geology, fossil lagerstätten were regarded as exceptions, as bizarre things; there were only about ten of them and they were a bit weird - Burgess Shale, Solnhofen and the rest; they were almost seen as embarrassments to the overall progression of our knowledge. Now, if you look at catalogues of lagerstätten there are hundreds of them and there are many intermediates. Now we have realised that these sites of exceptional preservation give us a picture of the true diversity with which we can compare other coeval sites that do not have such exceptional preservation. There are so many of them scattered through time that it is possible to join the dots from site to site to give an enhanced view of what life was like. Indeed, for certain organisms, particularly those of the Tertiary where we have living representatives, our understanding of the palaeobiology and diversity can be pretty good.

Even for organisms that are no longer around, such as the sabre-toothed cat the youngest skeletons of which are about 8-10,000 years old (not that long extinct, but there is nothing living like them), we must not decry the fossil record. We know with a great deal of certainty that we can read from the bone and the musculature how these animals operated and, with one or two exceptions, most people would accept the conclusions. A huge amount of confidence can be placed in this kind of reconstruction via mechanical studies, to the extent that animation can be added to bring these animals to life in a very dramatic way. I think a number of your speakers were proud to be involved with the BBC in films such as *Walking with Dinosaurs*.

I became focussed on this issue about ten years ago: how can we tackle this never-ending niggles about the quality of the fossil record? A well-known remark was made by J B S Haldane. He was perhaps one of the leading evolutionary biologists of the last century, certainly one of the great popularisers; he was a geneticist and many other things, on the staff at University College London. He was a great promoter, a proselytiser, for evolution at a time when people were discussing it tremendously because of debates about whether Darwinism was correct or not. Somebody after one of his lectures asked him "Professor Haldane, is there any fact which would shake your confidence in evolution?" He furrowed his great brow and the answer he gave was that if someone could show him a Precambrian rabbit (Figure 4), then he would have to doubt everything he had learned. I was very interested in his choice because he was not a palaeontologist and did not work in that field. He was primarily a geneticist and statistician and yet he picked that as the example because he saw it as such a fundamental part of evolution: the order of the fossils in the rocks. That is very important. It is more than just important to palaeontologists as a sort of minor detail. Haldane saw that the focal point to the whole business of evolution was that if you found that the fossil record was totally out of kilter with our understanding of evolution of life, it would be a big problem.

In the 1990s a number of people started to think that they now had the opportunity to look at the history of life using a variety of dif-



ferent lines of evidence: the order of fossils in the rocks, cladistics (the methods of creating branching patterns of relationships generally based on morphological features and which can include living and extinct organisms in the same pattern), and molecular phylogeny.

Independent data

In a simple sense these three are completely independent, however, there is a certain amount of linkage in that the choice of out-groups can control the nature of the cladogram that is obtained. There is no inclusion of any measure of age of the fossil organisms in determining this branching pattern; clearly, the molecules of any living organisms are totally divorced from the fossil record.

Likewise with the molecular data and, of course, there is never a neat and tidy result. It is very much a mathematical construct and does not include any input from knowledge of the fossil record. So the interesting question was to compare the information obtained from both.

We have information about order in time from the fossil record (A comes before B comes before C) but similarly, there is information about order in branching cladograms. A lower branching-point must occur before a higher one because if the pattern is correct there is no possibility that branches could occur in a different order. This can then be compared with the fossil record.

This was quite an exciting experiment when it was first done by Mark Norell and Mike Novacek (1992) of the American Museum of Natural History.

If you find that the cladogram agrees with the fossil record, then that would suggest one thing; if it does not agree that would suggest something else. The assumption here is that if they agree more often than not it implies that both the fossil record is good and the methods of making these cladograms are good, because the kind of sources of errors and biases (that affect the rock record and the fossils in it and the molecular data and the way you make the trees) are quite different. To get congruence with them both being wrong is quite unlikely. If, on the other hand, they cannot be made to agree (that on the whole they are telling a quite different story) then it is not possible to deduce what has gone wrong. It could be the fossil record that is wrong or the cladogram-making technique is wrong, or indeed that both are wrong.

So what was found in this first study? Happily (I would not be here otherwise) 75% showed agreement. What Norell & Novacek (1992) did was to sample surveys of published phylogenies of different groups of mammals and they plotted the order of fossils on the x axis and the order of branching-points on the y axis; if there is total agreement (as is obtained for horses) the result is a straight line graph with a slope of one. Many other groups, e.g. primates, do not show very good agreement and there is a scatter of points; it could be the fossil record that is incomplete or it could be that the reconstructed cladogram is incorrect. That 75% of them agreed was actually very gratifying because this suggested that a) the fossil record of these mammal groups was quite good and that the order of fossils is actually the true order of appearance of these creatures and b) that the cladogram-making techniques were working.

In Bristol we have had a programme running for the last five or six years, trying to extend this further. We decided to base the data on a single source, the *Fossil Record 2* (Benton 1993): a vast compilation by about a hundred authors of everything that was known about the fossil record. We used this book as a standard so that people can check and cross-check. We also used a variety of different ways of comparing cladograms with time the first of which was the Stratigraphic Consistency Index which compares the assumed date of each branching-point based on the knowledge of the fossil record; they are tallied as consistent or inconsistent and come up with a ratio.

We also used a standard stratigraphic range chart marked in time divisions of families and genera. The resulting graph shows the known fossil ranges and the so-called ghost range. The ghost range is the range implied by the shape of the cladogram which can extend the range of a fossil well below its known stratigraphic occurrence. If the fossil record is very incomplete you have an awful lot of ghost range.

The final method is a model which was invented by Matt Wills (1999), who was working in Bristol at the time. He took the real tree and compared it with a situation where he changed the relationships in the cladogram to try to maximise and minimise the amount of ghost range.

We compiled a thousand cladograms and molecular trees and measured these with Matt Wills's software. We thought a thousand was a reasonable sample; it covers all groups of plants and

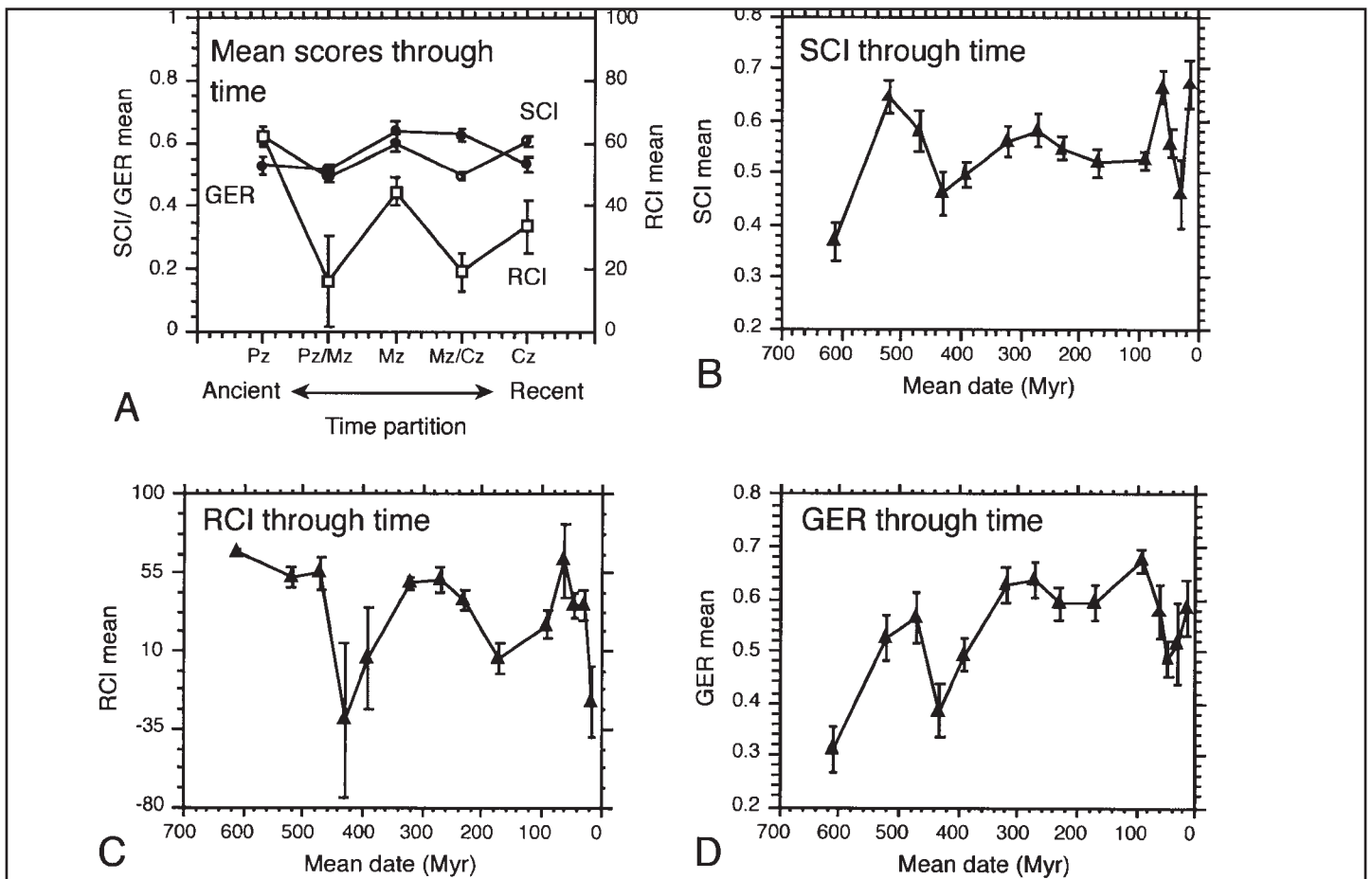


Figure 5. No change in fossil record quality through time, mean scores of the age vs. clad metrics for finer-scale divisions of geological time. A, Stratigraphical consistency index (SCI), the Relative completeness index (RCI), and the Gap excess ratio (GER) for five time partitions of the data set of 1000 cladograms, namely cladograms with origins solely in the Palaeozoic (Pz), cladograms with origins spanning the Palaeozoic and Mesozoic (Pz/Mz), cladograms with origins solely in the Mesozoic (Mz), cladograms with origins spanning the Mesozoic and Cenozoic (Mz/Cz), and cladograms with origins solely in the Cenozoic (Cz). B-D, Age vs. clad metrics for cladograms partitioned into geological periods and epochs, showing temporal variations in the SCI (B), RCI (C), and GER (D). There is no statistically significant secular trend for the broad-scale time divisions (A), nor for the period-by-period assessments by the SCI (B) or RCI (C). The GER values (D) do improve through time ($0.5 > p > 0.025$), but the regression becomes non-significant if the low Vendian value (based on 34 trees) is omitted. Based on Benton *et al.* (2000) and subsequent work.

animals from all sorts of ages including a lot of molecular trees, and trees of all sizes.

The question was: was Raup correct or was Valentine correct?

If this method is used to try to relate cladograms to stratigraphy it might be expected that, if Raup was correct, the quality of matching congruence values would diminish with age. If, on the other hand, Valentine was correct and it was reasonably valid to plot these diversity curves, assuming that our knowledge of the Palaeozoic was reasonably good, it would be expected that they would remain fairly constant; and constant they remain.

So we (Benton *et al.* 2000) divided up these thousand trees into five bins of approximately two hundred each, from Palaeozoic to Cenozoic, plotted the means with error bars and found that they do remain constant, though not specifically time-related (Figure 5). The RCI diminishes through time, but the older trees cover a lot of known range running right up to the present date. There is

a bias in favour of the older trees but I am inclined to discount it because it is time-related.

There are two points I have to make here. First of all we know very well that if we go to a Miocene or Pliocene site it is bursting with fossils, Jurassic sites are almost as good. There is nothing like that for a Cambrian or Ordovician site (apart from the Burgess Shale). There is a difference of focus. When collecting in the field individual specimens are collected from an individual locality; here we are looking at families and long periods of time, not at individual sites or even individual zones. So there can be a poor knowledge of species but a good knowledge of families. There may be only two or three known species in a family of trilobites, but two of them are enough evidence that such a family existed. It is partly to do with averaging.

I think we are happy that we are looking at a representative sample of the fossil record as it is in the rocks, but we still have not tackled the question of how good is the fossil record in represent-

ing life as it actually existed through time. This can probably never be answered, but note that in our study we included many molecular trees, so there is no difference between hard-bodied and soft-bodied organisms. I would argue that if there is agreement between the fossil record and phylogenies which include soft-bodied organisms it suggests that the known fossil record is not horrendously distorting what happens and that we can have a modicum of confidence that it actually represents the true history of life.

This mismatch between molecular and morphological data is an interesting debate that will carry on for a few years. My view is that we do not have to take strongly contentious positions. There are plenty of problems with the fossil record we can recognise and that, equally, there are plenty of problems with the molecular approaches which I think are increasingly being recognised.

There are several arguments against the suggestion that half the fossil record is missing. One argument is that the missing early representatives of animals that we do not find in the Precambrian are absent because they are soft-bodied or small. However, we cannot use that argument for these apparently-missing penguins and camels in the Cretaceous, because there cannot be a situation where these groups went through a soft-bodied stage then acquired their skeletons. In other cases, e.g. the bird/mammal case and some of the plant cases there is a similar mismatch, there are fossils throughout. The point is that throughout the Cretaceous, where these putative protopenguins and protocamels are supposed to be, there are plenty of small mammals and birds and some of these fossils are spectacularly preserved. So we will never know for sure but it is improbable that these things would be unpreservable.

This is the 'missing mastodon' argument. Around 1750, when people found huge elephant bones and teeth in Ohio, many people suggested 'Ah well, they are living in the more distant reaches of North America'. When they finally get out to the West they are going to find these extraordinary creatures. People have looked very hard but they have not found them. You cannot say absolutely that they are not there, but the probability is very high that they are not. My suggestion is, that as the years go on and we fail to find early Cretaceous parrots and penguins and camels, the less likely it is that they ever existed. But it is not an absolute argument.

I think there are other issues to do with the molecular clock: it is not a steady phenomenon and more thoughtful molecular biologists are looking at the suggestion that during dramatic phases of evolution (what we often call evolutionary radiations) the molecular clock speeds up; perhaps it is somewhat adaptive. Hence if it runs fast during a radiation in the early Tertiary there will be a lot of differentiation molecularly amongst the different groups of birds and mammals. If you then impose an apparently steady clock, that will then extend those periods too far back.

I think the mammal case is already resolved. A lot of the problems are defining what is really meant by different orders, different superorders, and so on. In fact there is now a mis-match of only about 5-10Ma between the currently accepted molecular dates and the currently accepted earliest fossils.

Although there are no mammals belonging to modern orders in the Cretaceous, there are placental mammals in the Cretaceous that belong to modern superorders: e.g. generalised ungulates. They take the record back down to about 90Ma ago and the molecular people have been rewriting, recalculating and recalibrating and those dates are coming up so, as the fossil dates come down a bit and the molecular dates come up a bit, there is a good convergence now for dating the mammals. I suspect that the same as that will happen with a many of the other disputed dates: it is a good way of getting your paper into *Nature* to say that 'the fossil record doesn't work and here is a new way of looking at it'.

So overall, I would like to suggest that we should have confidence in the fossil record, not only in the artistic reconstructions, but also that we can accept that our understanding of relationships of the larger patterns in their diversity through time are actually well-informed by the fossil record.

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Insects – a group beyond census

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Kingdom	Animalia
Phylum	Arthropoda
Superclass	Hexapoda (insects in the broad sense)
Orders	about 43
Families	over 1500
Genera	?
Species	1-20 million

Figure 1. Insects – systematic position.

Introduction

Insects (or Hexapoda – ‘six legs’ – to give them their proper name, Figure 1) are the most successful organisms on Earth if we measure diversity as a count of the number of species (biodiversity). Something like a million species of insects have been described in the last two and a half centuries (Figure 2a). Insects are also the most successful group in the fossil record if we measure palaeodiversity as a count of the number of families, as many palaeontologists do (Figure 3).

How many insects are there? Nobody knows for sure, although all estimates suggest that millions of insect species remain to be described. The great majority of these live in exotic places outside the UK. It seems unlikely, however, that description will keep pace with global habitat loss and extinction brought about by human development. Simple extrapolation from the fossil

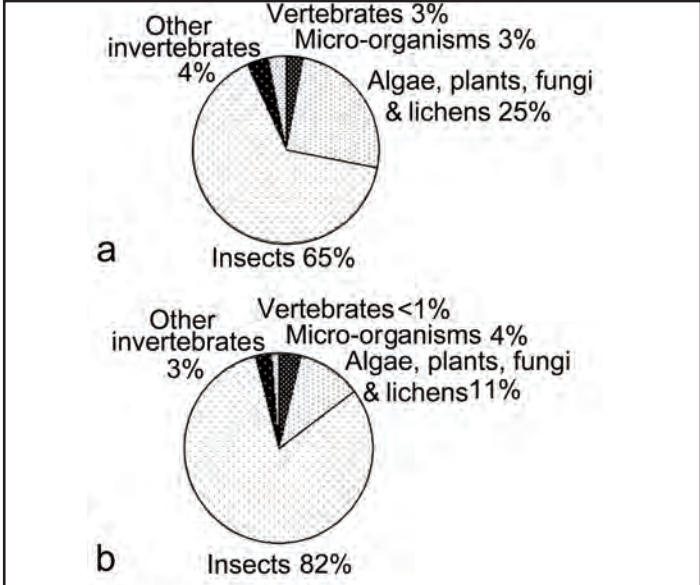
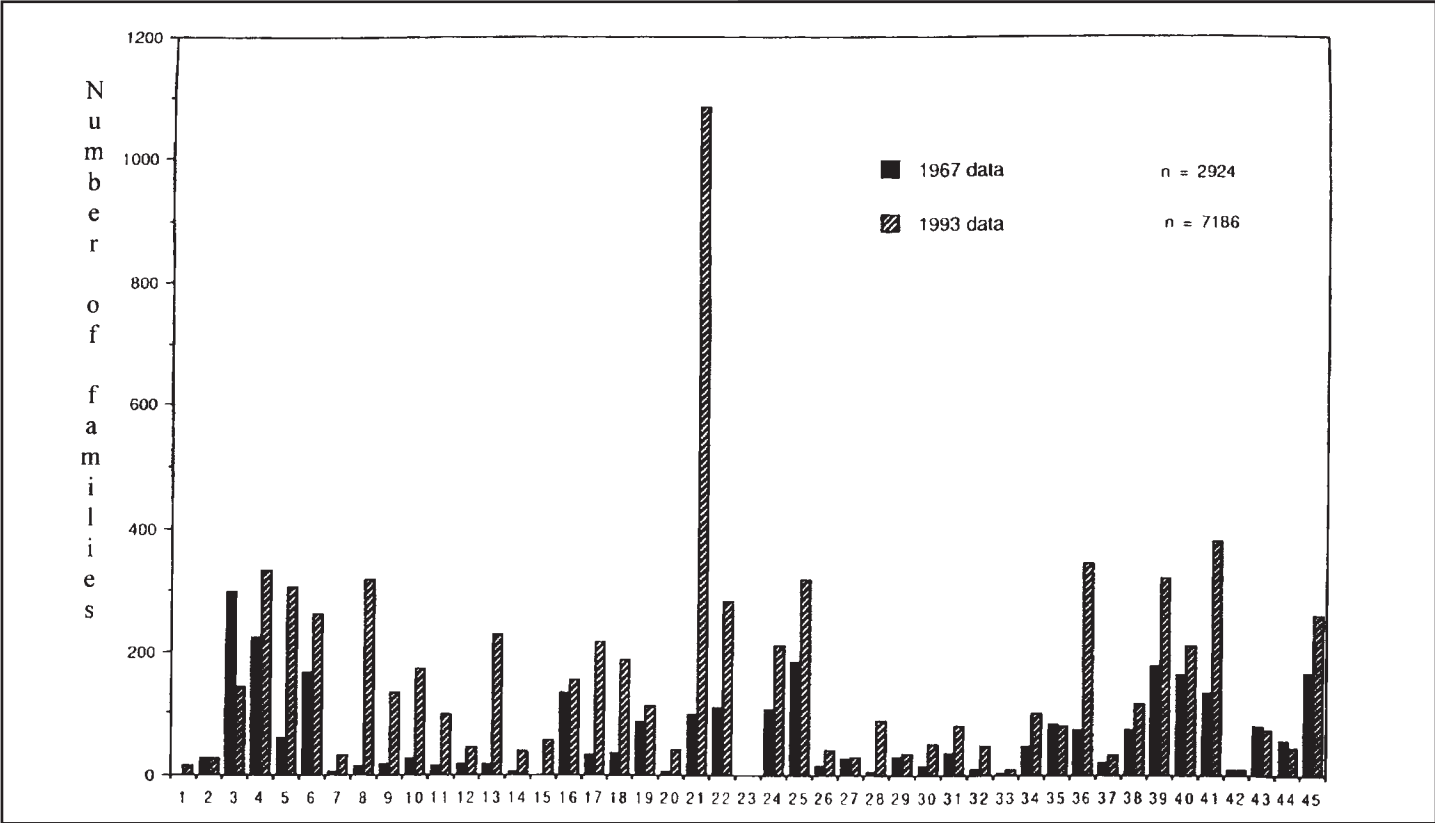
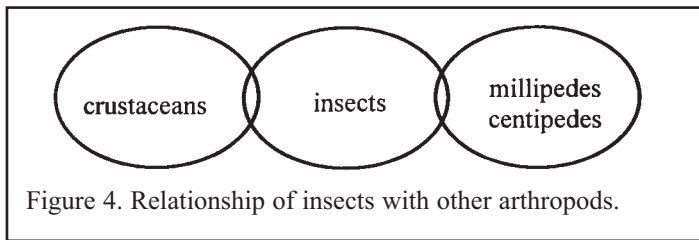


Figure 2. Global biodiversity pie charts showing percentage breakdown for insects and other organisms (after the Earl of Cranbrook 1996, and Wilson 1992): a) approximate number of known species worldwide (1,454,000). Insects are 65% of all known species; b) estimated total species worldwide including those remaining to be discovered (65,654,000). Insects are an estimated 82% of all species on Earth.

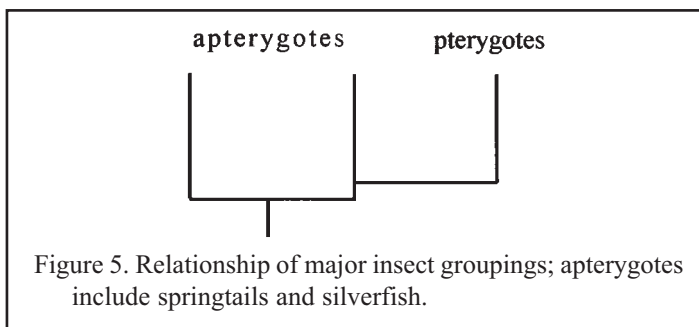




record suggests that the total number of insects is probably less than twenty million species (Jarzembowski & Ross, 1993: figure 9 caption fig. 10!), although some biologists prefer a higher figure. Everyone is agreed, nevertheless, that insects represent well over fifty percent of all known species and that they belong to an exclusive group of organisms described as hyperdiverse.

Origins

Where do insects come from? Insects are undoubtedly a class of arthropods or 'joint-legged' animals (Figure 1). Arthropods also include trilobites, crustaceans (prawns, etc.), chelicerates (spiders, etc.) and myriapods (millipedes and centipedes). Insects show closest relationships to crustaceans (e.g. in the structure of their compound eyes) and myriapods (e.g. in their tubular or tracheate respiratory system) (Figure 4). The exact relationships are currently a subject of debate.



Classification

Insects are divided into two main groups – winged and wingless hexapods (Figure 5). The wingless (apterygote) insects are a mixed bag and only some (silverfish) are thought to share a common ancestor with winged (pterygotan) insects. The pterygotes are divided into two main groups (Figure 6) – those which can fold their wings over the body (Neoptera) and those which cannot (Paleoptera). The neopterans, in turn, can be divided into two groups – those with complete metamorphosis (Holometabola) and those with incomplete metamorphosis ('cockroach – grasshopper')

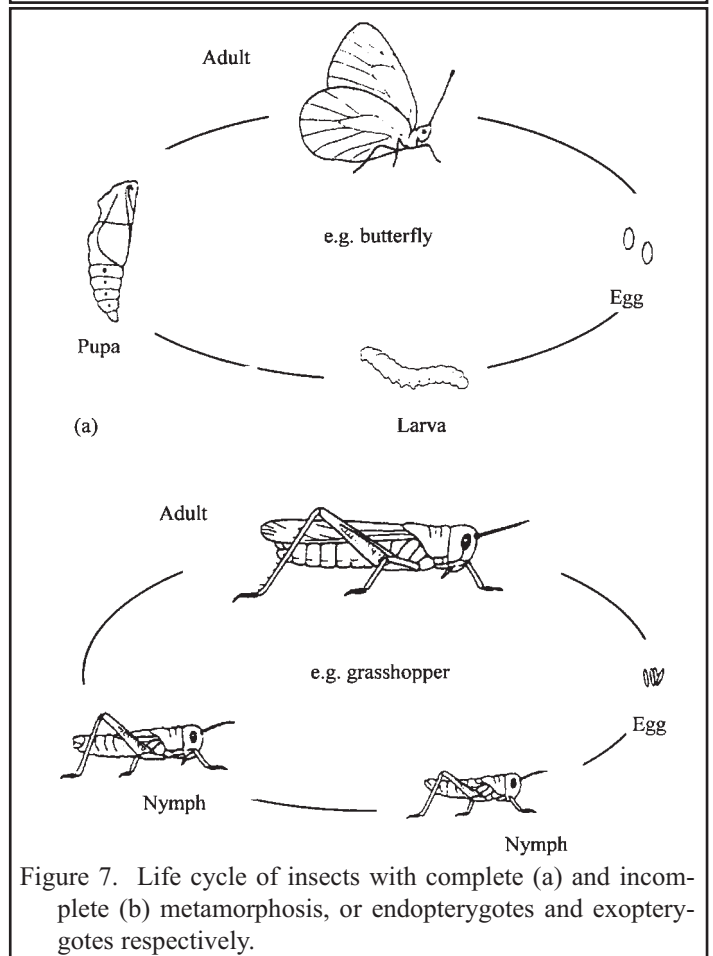
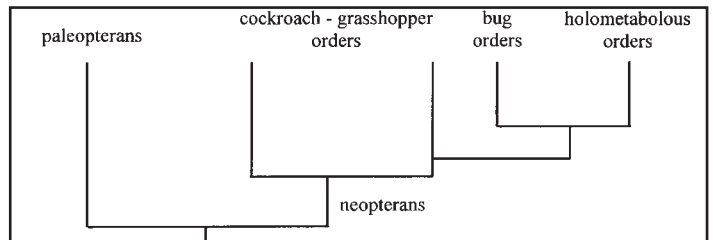
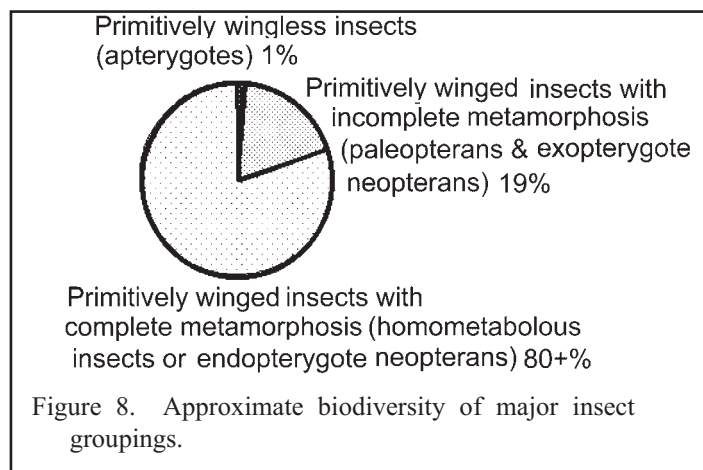


Figure 3. Palaeodiversity of organisms (after Benton, 1993).

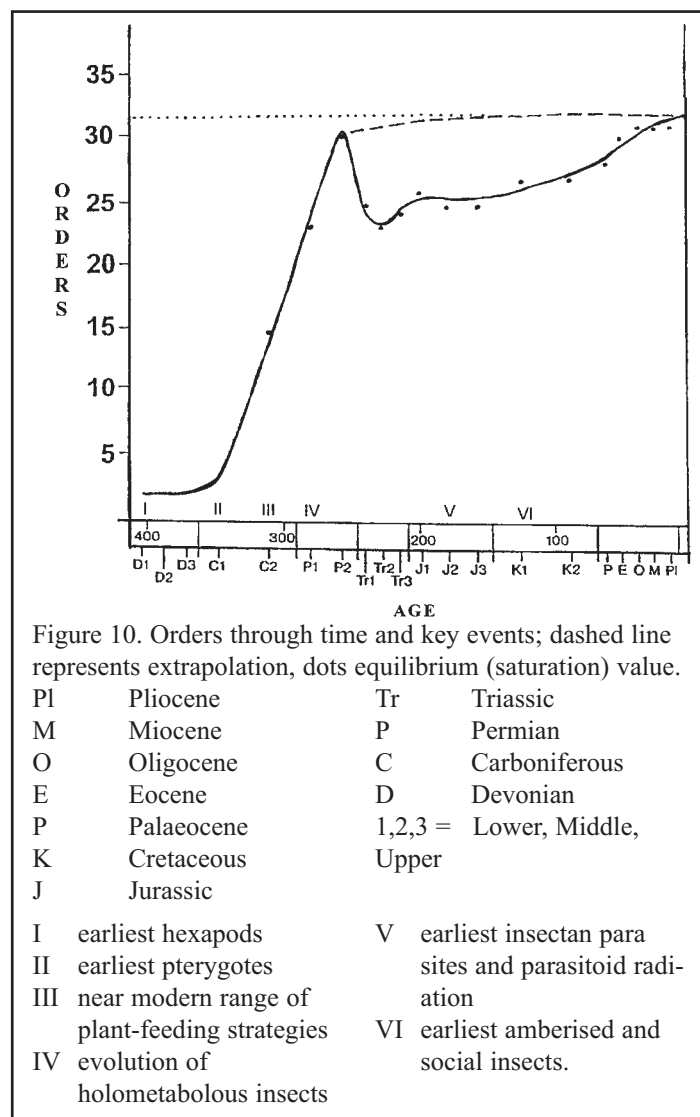
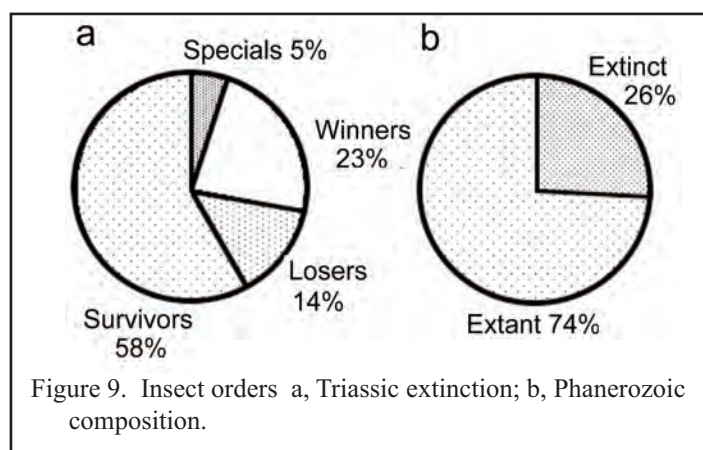
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|-------------------------------|-------------------------------------|-------------------------|----------------------------|
| 1. Bacteria, blue-green algae | 13. Bivalves and tusk shells | 24. Moss animals | 36. Advanced bony fish |
| 2. Fungi | 14. Uncertain molluscs | 25. Sea urchins, etc. | 37. More bony fish |
| 3. Other algae | 15. Segmented worms | 26. Primitive chordates | 38. Amphibians |
| 4. Single-cell organisms | 16. Trilobites | 27. Graptolites | 39. Reptiles |
| 5. Sponges | 17. Spiders, etc. | 28. Problematica | 40. Birds |
| 6. Corals, etc. | 18. Crustaceans except seed shrimps | 29. Miscellaneous | 41. Mammals |
| 7. Chitons, etc. | 19. Seed shrimps | 30. Conodonts | 42. Mosses, etc. |
| 8. Snails | 20. Millipedes, etc. | 31. Lampreys, etc. | 43. Ferns, etc. |
| 9. Nautiluses | 21. INSECTS | 32. Cyclostomes | 44. Seed plants except ... |
| 10. Ceratites | 22. Lamp shells | 33. Primitive fish | 45. Flowering plants |
| 11. Ammonites | 23. Phoronids | 34. Sharks, etc. | |
| 12. Belemnites | | 35. Primitive bony fish | |



and 'bug' orders); the latter are also known as exopterygotes because the wings develop on the outside in the young stages (Figure 7). In contrast, the wings develop inside holometabolous insects or endopterygotes. In holometabolans, the chrysalis or pupa is the 'resting' stage between the caterpillar, maggot or grub and the flying adult. The holometabolans are the most diverse insects and apterygotes the least (Figure 8). Some pterygotes have, however, lost their wings, e.g. fleas. Very high diversities (100,000 or more species) are only reached in four (holometabolous) orders: beetles (Coleoptera), moths and butterflies (Lepidoptera), wasps, ants and bees (Hymenoptera), and true flies (Diptera).

Geological History

The origin of insects is a bit of a mystery, the Cambrian Burgess Shale arthropods being too early to cast any light on the subject. The oldest hexapod is *Rhyniella praecursor* Hirst & Maulik from the early Devonian Rhynie Chert. *R. praecursor* is a springtail belonging to the living apterygote order Collembola. In the latest Lower Carboniferous and Upper Carboniferous we see the radiation of the pterygotes including paleopterans and 'cockroach-grasshopper' orders. These insects were the world's first flying animals, long before vertebrates took to the air. In the succeeding Permian, the 'bug' orders and holometabolans became established. Insects are essentially terrestrial organisms, but the first fresh water forms appeared in the Permian. After a setback in the early Triassic extinction (Figure 9), insects regained their ordinal strength by the Tertiary establishing some innovations on the way, e.g. evolving parasitic and parasitoid forms as well as insect societies (Figure 10). The extinction at the start of the Mesozoic seems to have been the biggest in insect history, although losses were not really catastrophic. Indeed, the successful order Diptera



(true flies) arose in the Triassic (Fig. 9 - Specials). It showed, however, that even hyperdiverse organisms are affected by global environmental change.

Collecting and documentation

Just as there are millions of insects to be described in today's hot countries, so there are thousands of fossil species to be described in places like the UK which were once warmer. The collection and documentation of fossil insects is of scientific as well as cultural value. It is possible to find more new fossil insect species on one field trip than in an entire lifetime's collecting of more popular fossil groups like vertebrates. Fossil insects are thus an ideal group for finding something new (and usually require less storage space on account of their small size). In the UK, insects may be found in the Coal Measures, Rhaetic, Lias, Purbecks, Wealden and a number of Lower Tertiary horizons. They also occur as sub-fossils in the Quaternary. These deposits span most of insect history. Our knowledge of the pre-Quaternary record was largely forgotten with the passing of the pioneer Victorian geologists and naturalists. There is now, however, a revival of interest, the wider search for Carboniferous pre-Namurian insects being of paramount importance.

If you have a healthy bank account, then you can also purchase a fascinating variety of foreign fossil insects at fossil and mineral fairs. These markets take place every weekend somewhere in the

UK. Thanks to internet communication and international trade, dealers can offer you new material which has yet to find its way into museums. There are New and Old World resins and ambers available (beware of misidentification), and a variety of rock fossils.

Even if you are not a collector, there is scope for documenting fossil species, e.g. sorting and conserving existing collections (especially little-known ones in regional museums), inputting web information, and translating key bits of description in foreign languages.

Literature

The only *Palaeontographical Society Monograph* on fossil insects is that on the Upper Carboniferous by Bolton (1921-2). It is beautifully illustrated with photographs. Two more modern illustrated books (relying mainly on line drawings) are Carpenter (1992) and Rohdendorf & Davis (1991). The latter has recently been augmented by Rasnitsyn & Quicke (2002). However, they only go down the Linnaean hierarchy as far as genera in anything like a comprehensive way. Amber inclusions have spawned their own colourful literature, e.g. Weitschat & Wichard (2002). Fossil insects are beginning to appear in regional field guides and natural history books, e.g. Swift & Martill (1999) and Jarzembowski (1999) respectively. And, of course, there are sites beginning to appear on the Internet, e.g. Meganeura, International Palaeoentomological Society (I.P.S.).

The Future

For logistic reasons, the study of fossil insects (palaeoentomology) relies on international co-operation which resulted in the founding of I.P.S. in September, 2001. OUGS could help individually or by involving whole branches. Some challenges are outlined below.

Mainland Europe

There are no Permian insects known from the U.K. Can the gap be filled on the Continent, or by looking for suitable deposits here?

Ireland

Early pterygote insects occur in the Namurian Clare Shales near Doolin, County Clare, but are little known. Is anyone willing to prospect for more?

W. Scotland/Oxford

Early Tertiary insects are generally uncommon but have been found with plants in the Interbasaltic Beds of Mull and Reading Beds of Berkshire. Has anyone looked for insects in these Tertiary plant beds?

E. Scotland

The earliest hexapod is from the Lower Devonian Rhynie Chert of Aberdeenshire. There are no pre-Namurian winged insects known anywhere. Has anyone looked for insects in the local Devonian or Lower Carboniferous?

Gogledd Cymru/W. Midlands/Severnside

There have been significant finds over the years from the Upper Carboniferous (e.g. South Wales Coalfield) and Triassic-Jurassic (e.g. Rhaetic outcrops along the River Severn). Has anyone looked for insects recently?

North West/Northumbria/Yorkshire/E. Midlands

Why are there so few fossil insect records from northern England, e.g. coastal Jurassic outcrops?

Walton Hall

There are nineteenth century records of insects in the Jurassic and Cretaceous to the north and west of London, e.g. Stonesfield Slate, Purbeck Beds. Has anyone found any recently?

South West/Wessex

There are diverse insects to be found in the Triassic (e.g. Axmouth), Jurassic (e.g. Charmouth), Cretaceous (e.g. Isle of Wight) and Lower Tertiary (e.g. Bognor Regis) plus various nineteenth-century records (e.g. Bovey Tracey). There is one person investigating Purbeck insects ... Are you ready for team working?

E. Anglia

The coast is a classical source of British Baltic amber. Has anyone found any insect inclusions?

London/South East

There are insects to be found in the Lower Cretaceous (e.g. Wealden) and Upper Carboniferous (Kent Coalfield). Sites are, however, prone to redevelopment. Is anyone collecting while it is still possible to do so?

Conclusion

I hope that some or all of you will pick up the fossil insect challenge.

If you're looking for a fun activity with a geological purpose, then palaeoentomology could be for you. And even if it's not, at least you now know that it's insects which really dominate the Earth...

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Web sites:

INTERNATIONAL PALAEOENTOMOLOGICAL SOCIETY
<http://www.cwru.edu/affil/fossilinsects/>

MEGANEURA
<http://www.ub.es/dpep/meganeura/meganeura.htm>

WEALDEN NEWSLETTER
<http://www.wealdennews.f2s.com>

Stop Press:

Visit 'wee beasties' on OUGS London website.

Book reviews

Architects of Eternity by R Corfield, 2001, Headline Book Publishing, 338pp, £18.99 (hardback) ISBN 0747271798.

It was the title of the book which caught my eye as I am fascinated by new discoveries or things that are interestingly different. At first the book was somewhat hard going but it became easier as it described names of researchers and details of 'discoveries' made in the past which are now known to be misleading. This book describes the findings of physicists, mineralogists and top graduates of other sciences who became palaeontologists employed in recognising new species and defining their place in the geological succession.

These researchers did their science the hard way but always supported each other. They worked with the newly discovered carbon isotopes and new instruments that could measure temperatures deep within the oceans. One researcher even built his own mass spectrometer which he used successfully for many years; very different from conditions today where the latest scientific instruments are available in most laboratories.

There are few illustrations but these include relationships between Gondwana, Laurentia the Tethys, Rheic and Iapetus Oceans. There are some portraits of famous people and a picture of the Lapworth microscope. It describes the Joint Oceanographic Institutions for Deep Earth Sampling, and the mid Cretaceous ocean stagnation.

It is an easy book to read, so if you are lost in your OU chemistry kit and wonder if it is really worth the effort, then clear away the kit, get some of your friends together, sit with your elbows on the table, heads on the hands and discuss the problems to see what theories you can come up with. Many scientific theories were worked out by people who thought about things and recognised what was possible. They are an inspiration to us all and should not be forgotten.

Helma Tasker continuing OU Earth Sciences student

Classic Landforms of the Brecon Beacons, Richard Shakesby, Geographical Association with the British Geomorphological Research Group, 2002, 48 pp, £8.95 (paperback) ISBN 1843770164.

"The Brecon Beacons National Park contains arguably the most spectacular upland scenery in southern Britain", begins this attractive little booklet. Even those of us for whom it is a daily sight don't tire of these striking Old Red Sandstone escarpments which dominate the upper Usk valley and part of the upper Wye valley. However don't expect to learn from this work how and when the major scarps and valleys were formed; it is scarp-foot landforms that the author is concerned with. Because it is the nature of glaciations to wipe out the results of their predecessors, these scarp-foot landforms are very recent: the result of the latest, Devensian, glaciation and of the Loch Lomond Stadial. There has been much work in recent years on these landforms; a relevant work was published on average every two years since C. A. Lewis' magisterial essay in Brycheiniog, 1970, according to the comprehensive bibliography Shakesby gives.

Shakesby confines himself to that part of the National Park south of the Usk; it is to be hoped that there will be a companion volume for the Black Mountains. He divides the area into three, "Fforest Fawr", "Mynydd Du",

and "Bannau Brycheiniog", although there is no particular difference between the processes and landforms of each, and rather oddly treats them in that order, central first, instead of east to west or west to east. On the general map of the "Brecon Beacons National Park" (actually only half the Park area, and without the Park boundaries) the names of his three divisions are confusingly in the same type as the peaks and crags.

There is a very clear introduction both to the ORS range of mountains and to the possible origins of scarp-foot landforms, and then a full description of every relevant site (nearly two dozen in all).

I have tried out his descriptions on two sites, those along the A470, north of the Storey Arms, Craig y Fro and Craig Cerrig-gleisiad. What he writes, and his clear diagrams, makes both the simple former and the very complicated latter extremely easy to understand. Landforms I had taken for granted for years became fascinating. I shall certainly buy this booklet and it will probably live permanently in my rucksack. Recommended for all of you who have the good fortune to come to these noble mountains!

Philip Clark BSc(Hons), MA (Oxon)

Rocks and Scenery of the Peak District by Trevor D Ford, 2002, Landmark Publishing, 96pp, £7.95 (paperback) ISBN 1843060264.

Trevor Ford has produced many books and papers about the Peak District which are all written in a deceptively simple style and packed full of facts. This book is no exception apart from the inclusion of numerous colour plates which greatly enhance the clear black and white diagrams, some of which are taken from earlier publications – but why reinvent the wheel? The material is aimed at non-professionals, presenting the landscape through the detective eyes of a geologist, always keeping jargon to a minimum with explanations of any necessary technical terms as they crop up.

The preface expresses the author's wish to present a story in two parts: firstly about the formation of rocks over 300 Ma and then how those rocks have been carved into the present day landscape by ice, wind and water all in the light of his 50 years experience in the Peak District. He acknowledges the re-use of earlier material and includes a good reading list for those who wish to find out more.

The rock story unfolds stratigraphically starting with the Lower Carboniferous Dinantian limestones of the White Peak, moving through toadstones, or volcanic lavas and ash, to the Millstone Grits of the Namurian. Then, chapters covering structures, minerals/mining and ice ages tell the later story of how the landscape was formed. Instead of including itineraries for field trips, a common format for such books, the later chapters are split into topics such as rivers and drainage, dry valleys, screes and landslips, peat and caves with many sites named as examples of each. Thus, you could easily make up your own field trip with ingredients to suit your taste.

The book ends with a chapter covering areas of special interest eg. Winnats Pass, Odin's mine, Kinder Scout, Robin Hoods Stride and Alport Castles to name but a few of the evocative names familiar to all who have grown to love this scenic part of the country with much geological interest. At a modest £7.95, which belies the quality of paper and colour reproduction, it would make an ideal present to encourage a new geologist or to complete a collection of Peak District literature.

Chris Arkwright, BA Hons (Open), MSc (Man),
OU tutor and continuing PhD student.

The fossil record of the Ginkgoales: form species and the limits to knowledge

David Scarboro, Associate Lecturer, Open University

About ten years ago I was on holiday in Canada and I went to the Royal Tyrell Museum of Paleontology at Drumheller, Alberta, to see the dinosaurs - specifically the dinosaur footprints from the Peace River, an area of Northern Alberta which had been flooded by a hydroelectric project. I wrote to them in advance and got a guided tour around the back, which was great and I saw a lot of fossil footprints. Out in the main museum they had a lot of fossil plants from Alberta, and I noticed there were a lot of *Ginkgo* leaves there along with a lot of other stuff such as *Metasequoia*. My interest was aroused because I had a couple of specimens of *Ginkgo huttoni*, which is the most common ginkgophyte from the Yorkshire Jurassic. I thought, "Wouldn't it be nice if I could get one or two examples from the Cretaceous of Alberta to add to my collection!"

It was then I discovered The Fossil Shop in Drumheller, which is the best fossil shop I ever saw. They had loads of local material, including *Ginkgo* and other plants including ferns, *Metasequoia* and angiosperms. On this and a subsequent trip a few years later I actually cleaned them out of Ginkgoes! I got all the good ones anyway! So I had the makings of a collection and decided I would really like to try to build on it. I would see how many fossils I could assemble to see if I could put together a representative collection of Ginkgoes through time. In order to do that I had to learn about the fossil record and evolutionary history of the Ginkgoes, so what I'm going to talk about is a little of what I've learned and some of the questions I have come up with.

Ginkgo biloba is the only living species of the Ginkgoales surviving today. You have probably all seen examples: *Ginkgo* trees are planted as ornamental trees and quite common in botanical gardens in the West. Also, in England you tend to find them in older neighbourhoods and gardens, particularly Victorian gardens. If you go to the United States you will find thousands of Ginkgoes planted along the main streets of New York,



Figure 1. *Ginkgo biloba*, Kew Gardens

Washington and Boston; they're not hard to find and very popular. *Ginkgo biloba* is a gymnosperm belonging to the Order Ginkgoales, Family Ginkgoaceae. There is another Family of the Ginkgoales called the Czekanowskiales which are known only through the fossil record and which are now extinct; they were a very noble group of plants, but I am going to restrict my talk today to the Ginkgoaceae.

The best place to start is with the living tree, *Ginkgo biloba*, (Figure 1) which I think has quite a lot to tell us about what we see in the fossil record. This is probably the most famous example of *Ginkgo* in the western world - it's the famous tree in Kew Gardens which was planted in 1762 from a seedling which was germinated in the 1750s. The Kew *Ginkgo* is about 25 metres high.

Where did the Ginkgoes grow in the geological past, and what do we know about their biology? There is a debate that has been raging for about 200 years now as to whether there are any wild Ginkgoes left in the areas of the Far East and China where their natural habitat is. The consensus seems to be that there are probably a few wild trees in some small areas of China which are preserved as nature reserves, but even there it is not actually certain that the trees are truly wild. What the trees in these areas seem to like is upland areas with well drained soils. There is a nature reserve in eastern China called the Tien Mu Shan reserve where *Ginkgo* occurs in a range of altitudes up a mountain; according to one authority it occurs in "disturbance-generated microsites, including stream banks, rocky slopes and the edges of exposed cliffs, all of which are locations where the effects of soil erosion are readily apparent." We have in Tien Mu Shan a population of *Ginkgo* trees which are living in a refugium - we should not infer necessarily that fossil forms lived in such confined or restricted areas.

Now an important point about these trees is that they are *dioecious*, that is to say, either male or female. The male trees produce catkins in spring which release pollen in the wind. In public places, where most trees in England are planted, it is difficult to find female trees because male trees are planted in preference. The female tree produces fleshy ovules in spring which are fertilized by wind-blown pollen. After pollination the ovules stay on the tree and the seed ripens inside the fleshy outer covering until about October, when they fall off. They are heavy, so that they stay where they fall unless something comes along to move them. With the living tree the seeds are distributed by people from garden centres and so on, but how they were distributed in the past is an interesting question possibly connected with the reason why nowadays the female trees are not usually planted in public places - the seeds (fruits) stink! This is because the outer fleshy part surrounding the seed contains butyric acid, which is also found in the human stomach. When the seeds fall on the ground they start to rot! There is one place in London where female trees are planted in public; at Seething Lane, near the Tower of London, on the site of Samuel Pepys's house, the Victorians built a little garden with a nice iron rail around the outside, and four *Ginkgo* trees, two male and two female, planted inside the railing. This creates the possibility that the females could be wind pollinated. I have vis-

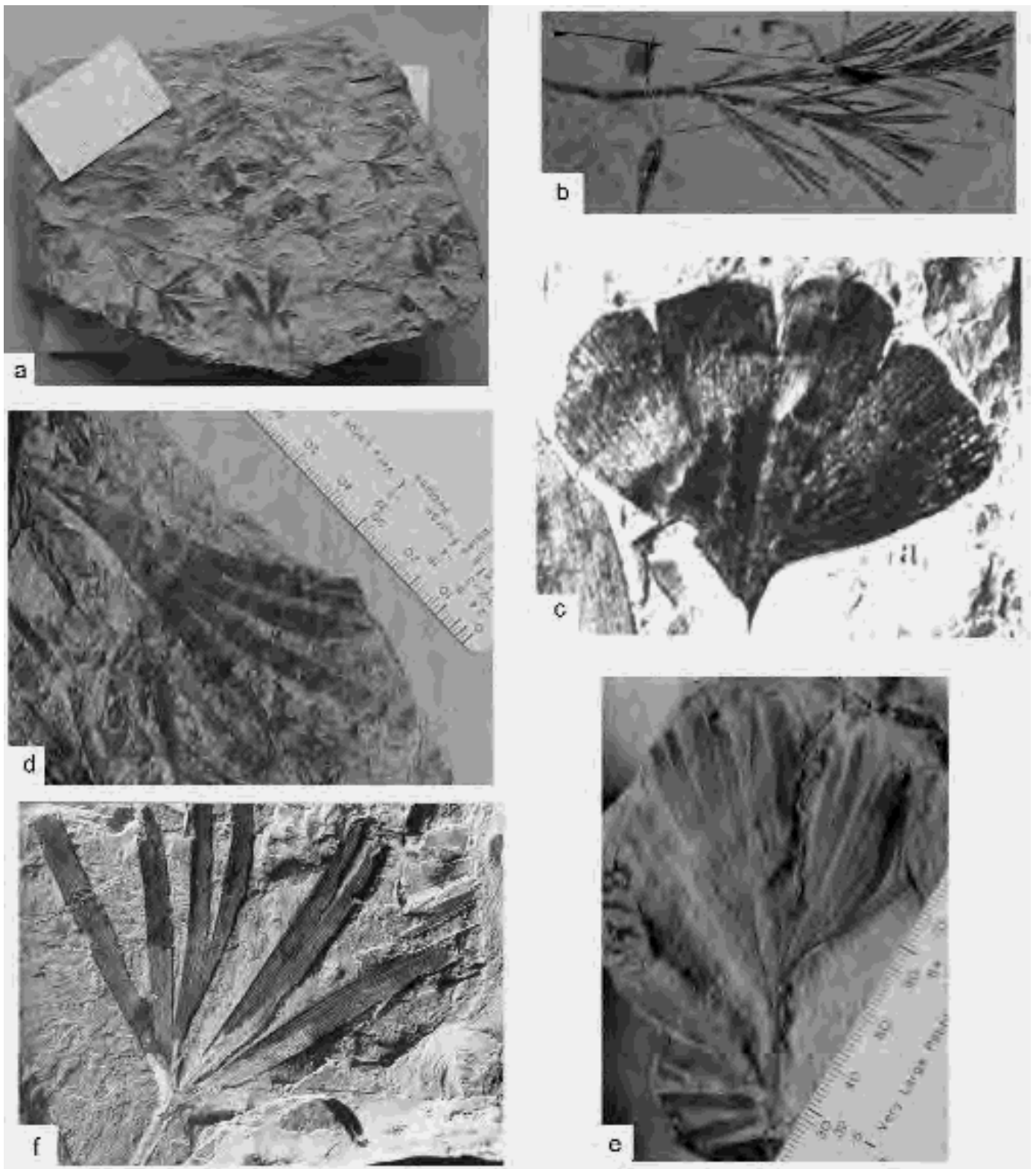


Figure 2. a) Leaves of *Ginkgo huttoni* crowded on a single bedding plane, Scalby, Yorkshire. b) *Dichophyllum moorei*, Carboniferous, Kansas, USA. c) *Ginkgo digitata*, Late Cretaceous, Alaska. d) *Sphenobaiera*, Late Triassic, Benolong, New South Wales, Australia. e) *Baiera manchurica*, Jurassic, Hunan Province, China.

ited Pepys Garden in October, collected seeds from the ground, and have got one of them to sprout. The downside of this visit was that there were thousands of seeds on the ground all rotting and stinking. I got on the Underground at Blackfriars with my shoes, trouser cuffs and jacket covered with yellow *Ginkgo* stuff and a little plastic seal-top bag with 130 dripping *Ginkgo* seeds inside. Needless to say, I was not very popular!

The implication of the smell is that the seeds may have been attractive to something that ate them. *Ginkgo*, as one writer has observed, may be a carrion-mimic! We don't know what animal or animals it was that ate the seeds, but in China today squirrels and other small mammals have been observed to eat them. The seeds are scarified in the gut and dropped somewhere else, giving a picture of turds with little *Ginkgo* seedlings growing out of them! We can assume that in the geological past, in the Tertiary and back into Mesozoic, the same thing was happening. Since mammals eat the seeds today, perhaps early mammals back in the Mesozoic were the culprits. We don't know - it could equally have been birds or small dinosaurs.

Ginkgo trees are deciduous, which is to say they drop their leaves in the autumn. The leaves become a brilliant golden yellow in early October; then they all fall off together in the space of two to three days. You tend to find *Ginkgo* trees in late October with a mass of leaves on the ground around them, and this tends to show up in the fossil record too, I think. Also, the leaves are rather heavier than the leaves of most angiosperms; they are covered with a fairly thick, waxy cuticle which gives them a high fossilization potential. This also means that the leaves can be transported rather easily by water, but they don't seem to blow around in the wind very well. I have observed a *Ginkgo* tree in Reading on a day when the wind was blowing around fifty miles an hour: all the leaves were on the ground close to the tree, and they weren't blowing very far.

Ginkgo produces two types of shoots on its branches. It produces long shoots where it lays down new wood every year; the long shoots produce a spray of leaves at the end. The other type of shoot is the spur shoot or peg shoot, and these are built up by scales or scars from the leaves season by season, so they grow very slowly.

A few words about the architecture of the typical *Ginkgo* leaf. Typically less than 20cm across, a leaf has two parts - the stem or petiole which is attached to the branch, and the lamina or blade of the leaf. The petiole is formed from two vascular veins arising from the branch, which separate at the top of the petiole to produce the lamina. Then each vein bifurcates or forks repeatedly to produce the web for the fan-shaped leaf. In *Ginkgo biloba* the forking of the veins goes all the way to the distal edge of the leaf. It is rather simple, rather primitive perhaps, lacking the complex net venation patterns of angiosperm leaves - trees such as *Archaeopteris* in the Devonian have the same kind of leaf architecture broadly speaking.

The leaves of *Ginkgo biloba* are very variable - you can see that for yourself on any *Ginkgo* tree. The leaves have two basic forms - what people normally think of as a typical *Ginkgo* leaf is a fan-shaped leaf with a notch in the distal margin. The other form is wedge-shaped and tends to be much more deeply notched than the fan-shaped leaves. The wedge-shaped, deeply notched leaves tend to occur on the long shoots and the fan-shaped leaves on the short,

peg shoots. So *Ginkgo biloba* produces two leaf morphs - fan-shaped, broad-bladed leaves and deeply notched or segmented, wedge-shaped leaves. Fossil leaves of Ginkgoales also seem to show a pattern of two leaf morphs occurring together, suggesting that the production of different leaf forms on long and short shoots is a long-standing feature of the group.

The fossil record of the Ginkgoes extends from the Permian to the Quaternary, a period of about two hundred and ninety million years. Nearly all Ginkgoale fossils are leaves, which is not surprising given that a single tree produces millions of leaves but just one trunk. Petrified wood is common in the fossil record, but, oddly, the Ginkgoes have left very little wood - the only fossil *Ginkgo* wood I have heard of is from the Miocene of the Columbia Plateau, at a little place called Ginkgo Petrified Forest in Washington State, in which rare trunks of *Ginkgo* occur in a petrified forest consisting mostly of conifers and cypresses. I have heard rumours of *Ginkgo* wood of similar age occurring in Nevada but have not been able to verify this. For the whole of the Mesozoic I have not been able to find documented evidence of any *Ginkgo* wood whatsoever.

The reproductive structures of Ginkgoes are also quite rare in the fossil record: the male catkins are fragile and do not tend to fossilise very well, but the seeds are fairly robust, so once they have ripened the fleshy exterior harbours a seed inside which does fossilise quite well, and we find these in rocks in western North America of Cretaceous and early Tertiary age. You do sometimes find *Ginkgo* leaves along with seeds, but the combination is rare, and in general it is usually difficult to match up leaves with reproductive structures in the fossil record.

When you find one fossil *Ginkgo* leaf you tend to find hundreds, even thousands. As mentioned before, *Ginkgo biloba* tends to drop all its leaves at once, and if there happens to be a stream or a depositional environment such as a lake nearby, the fossilization potential of autumn leaf-fall can be very high. The leaves tend to be transported quite well by water when compared to other leaves, so you sometimes find that *Ginkgo* leaves have survived transport in high-energy environments such as rivers when the leaves of other plants have not, giving sediments full of *Ginkgo* leaves and little else, even though adjacent low-energy sedimentary environments may preserve evidence of a diverse flora. In lake sediments *Ginkgo* leaves are often preserved with other types of leaves, with the whole palaeoflora represented. A geologist of the US Geological Survey reported in 1959 on a site in Miocene rocks in an old road cutting in the Columbia Plateau where he found what he describes as the latest known occurrence of *Ginkgo* in the Western hemisphere. He recorded that "*Ginkgo* leaves are preserved in a brown ashy clay of fluvial origin", and thought it seemed possible "that the abundance of leaves results from a single tree or a group of trees where their branches extended out over the stream." That is an illustration of the way you sometimes find these fossils with large numbers on one bedding plane in one place (Figure 2a).

We know little about the origins of the Ginkgoales. Since they occur in the Permian they probably originated in the Carboniferous - there's probably a Carboniferous ancestor somewhere waiting to be found. It has been claimed that this plant, called *Dichophyllum moorei*, (Figure 2b) which comes from the Carboniferous of eastern Kansas, is a candidate. It looks rather like the plants that Professor Challoner was showing us yesterday - instead of leaves

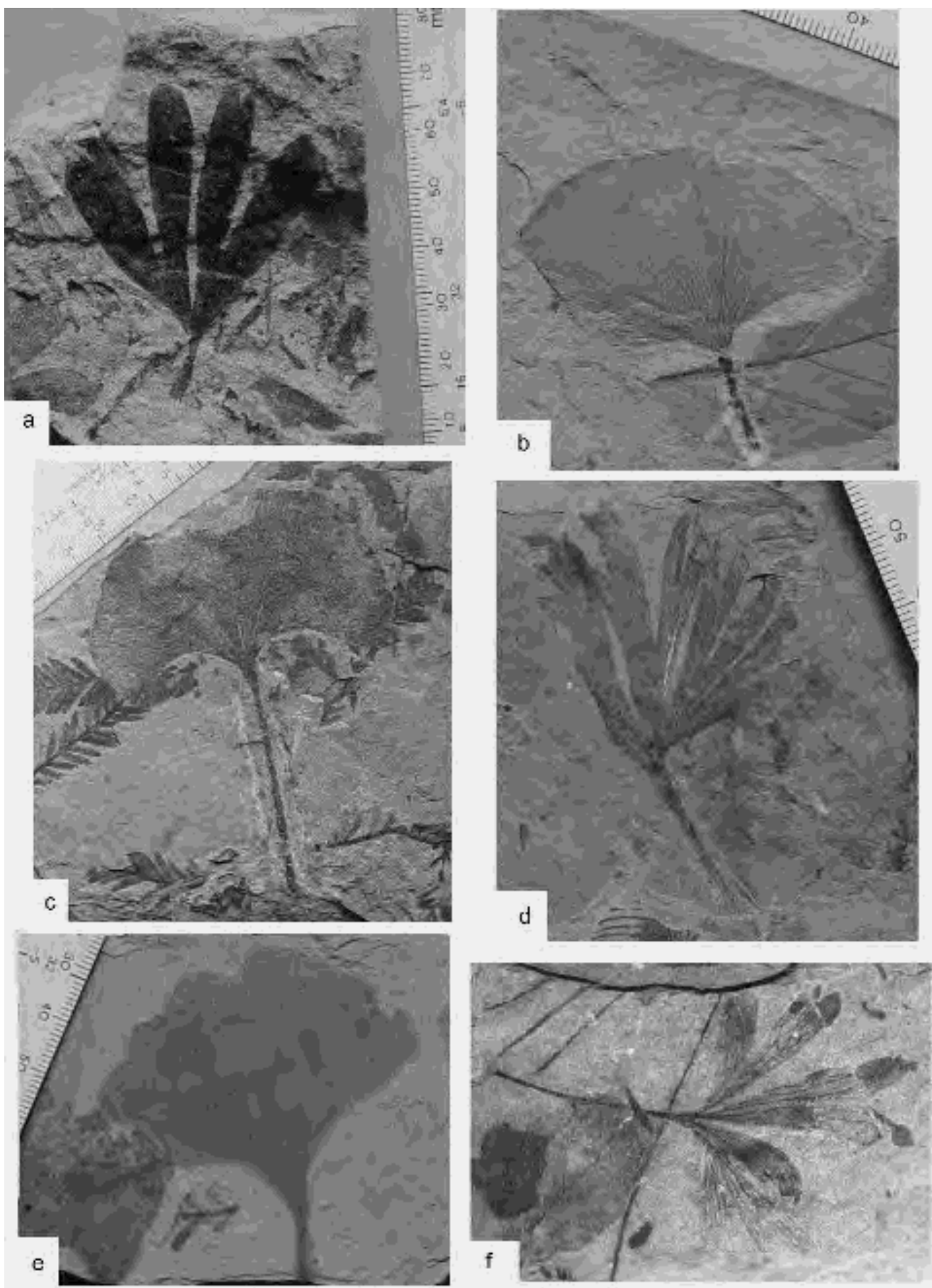


Figure 3. a) *Ginkgo huttoni*, Middle Jurassic, Scalby, Yorkshire. b) *Ginkgo adiantoides*, Eocene, Idaho, USA. c) *Ginkgo adiantoides*, Late Cretaceous, Alberta, Canada. d) *Ginkgo* sp., Late Cretaceous, Alberta, Canada. e) *Ginkgo adiantoides*, Eocene, British Columbia, Canada. f) *Ginkgo dissecta*, Eocene, British Columbia, Canada.

it has photosynthetic branches. It has been suggested that if you put webbing between the branches you get a sort of *Ginkgo* leaf. *Dichophyllum* looks like a model of what you might predict an early Ginkgoale to look like. Another possible early Ginkgoale is a plant called *Tricopitys heteromorpha*, from the early Permian of Provence. Its leaves are arranged in a spiral pattern on the stem; they resemble the leaves of primitive Ginkgoales from the Late Permian, so there is a possibility that *Tricopitys* is the oldest member of the Ginkgoales so far discovered.

I suggest that the earliest Ginkgoales probably lived in upland environments during the Carboniferous, when the supercontinent Pangaea was assembling. The formation of Pangaea caused a major change in climates on the land, from moist environments on vast coastal plains which could support the great coal swamps to more arid, continental environments. I think the Ginkgoes were pre-adapted to take advantage of this change, which may explain why the main adaptive radiation of the Ginkgoales occurred during the late Permian.

There are two different ways to look at the evolution of the Ginkgoes. The first way is to try to work out the evolutionary relationships within the group. It became apparent to me that you cannot do it on the basis of leaves alone - one leaf-form gives rise to another, but without the rest of the plant any apparent relationships may not be valid.

The second way to look at *Ginkgo* leaves is for the environmental information they contain. Plants are extraordinarily sensitive to changes in their environment, and with the Ginkgoes, although it is difficult to follow evolutionary relationships from one leaf-form to another, nevertheless there is a general tendency in the Mesozoic for *Ginkgo* leaves to develop from narrow strap-like leaf-forms to more whole-bladed leaves. It seems possible that leaf form was tracking climate change in the Mesozoic. I think the more strap-like, thin-bladed leaves were an adaptation to arid conditions, and that as Pangaea broke up, giving a greater variety of climates in the interior of what had been a single, giant landmass, the Ginkgoes responded to the relaxation of water stress by increasing the photosynthetic area of their leaves.

Fossil leaves are assigned to form species and form genera. A form species or genus is defined on the basis of morphology alone, and assigning form species is essentially an admission that the fossil record does not allow us to unravel the explicit taxonomic history of a group. Form genera and species are assigned Latin names under the Linnaean classification system just like the names we give to genuine biological species. This can be confusing because if you assign a leaf to a form species you do not mean to imply that all the leaves that belong to that form species are necessarily members of the same biological species. A very good example is a leaf called *Ginkgo digitata* (Figure 2c) which occurs in the Middle Jurassic of North Yorkshire and many other localities around the world.

Ginkgo digitata is an important Jurassic form with a global distribution - leaves of a similar age assigned to that form species are found in Oregon, but it is particularly noticeable that, especially in Alaska and western North America many leaves are assigned to *Ginkgo digitata* which come from the Late Cretaceous. I find it difficult to believe that a *Ginkgo digitata* from the Late Cretaceous of Alaska and a *Ginkgo digitata* from the Middle Jurassic of England, separated by about 80 million years of time,

could actually have satisfied the criteria of a biological species - if you put them together, a male from one and a female from the other, would they have produced viable offspring? 80 million years is a long time!

The situation as regards identifying true species may not be as bad as that because, as I mentioned before, *Ginkgo* leaves have thick waxy cuticles which, of course, have stomata. If you examine the cuticles under the microscope the shapes of the stomata and arrangements of the guard cells can be used to separate leaves out more reliably into biological species than the gross morphology of the leaves alone can do.

Palaeontologists are either lumpers or splitters. The Ginkgoes have tended to suffer at the hands of the splitters. More than twenty form genera have been assigned to fossil leaves, but recent work has brought the number down to about eight, and there are only four genera which are quite common and fairly representative. The form genus *Sphenobaiera* (Figure 2d) is the most primitive - it was very common in the Permian but it existed into the Late Cretaceous. The main characteristic of *Sphenobaiera* leaves that distinguishes them from other Ginkgoales is that they do not have a petiole - the leaves were attached directly to the branch, and grew and were shed together in sprays. The leaf is very wedge-shaped with very thin strap-like segments, each of which would carry between two and four vascular veins. The veins in the segments do not bifurcate or split.

A second form genus is *Baiera* (Figure 2e), a form which resembles *Sphenobaiera* except that it has a petiole. A large number of leaves are assigned to a third form called *Ginkgoites* (Figure 2f). There is a big debate about how to define *Ginkgoites* because there are many *Ginkgoites* form species which are indistinguishable from *Baiera* on one side and others that tend to bleed into the form genus *Ginkgo* on the other. Then we have *Ginkgo* itself, represented by *Ginkgo huttoni* (Figure 3a). The earliest fossil leaves assigned to *Ginkgo* appear in Siberia in the Early Jurassic; they are quite widespread by Middle Jurassic times, and starting to take over the world by the Late Jurassic and Early Cretaceous, pushing out the other forms.

Figure 3b is from the Eocene of Idaho. It is called *Ginkgo adiantoides* and it is very common in Tertiary and Late Cretaceous rocks - you can see that it is a whole-bladed leaf. *Ginkgo adiantoides* is often said to be indistinguishable from *Ginkgo biloba*, so the idea is that *Ginkgo adiantoides* survived into the Tertiary and ultimately gave rise to *Ginkgo biloba*. However, there are differences between early Tertiary *Ginkgo adiantoides* and the living *Ginkgo biloba*; also, cuticle analysis has shown that the apparently identical broad-bladed leaves of early Tertiary *Ginkgo adiantoides* may actually mask a number of genuine biological species, meaning that *Ginkgo adiantoides* is a multi-variant form-species.

Figures 3c & d are fossils from the late Cretaceous of Alberta, Canada. The fan-shaped leaf is *Ginkgo adiantoides*, but in the same beds alongside it is this segmented leaf with the segments divided almost all the way to the petiole. The question is, "Do we have two different biological species of *Ginkgo* living side by side in the same forest?" One possibility, by analogy with *Ginkgo biloba*, is that we have two different leaf morphs, one on long and one on short shoots, on the same tree. The same situation shows up in the Eocene of British Columbia, where very segmented leaves



Figure 4. *Ginkgo* sp., Palaeocene, Argentina.

Book reviews

Life at the Limit: Organisms in extreme environments. David A Wharton, 2002, Cambridge University Press, 307pp, £18.95 (hardback) ISBN 0521782120.

This is an enjoyable and up-to-date book about how life is able to survive in extreme environmental conditions. It describes the types of extreme environments found on Earth and the organisms that live there - principally deserts, salt lakes, soda lakes, the polar regions, mountains, the ocean depths, and deep underground. It analyses how organisms cope with the main types of physical stress that they experience there: desiccation, heat, cold, pressure, pH extremes, osmotic stress, lack of oxygen, radiation and toxins. The explanation is in terms of behavioural adaptations, physiological adaptations and molecular chemistry adaptations.

This journey around the extremes of biology gives easy access to large areas of biological knowledge and insight, and enables a deeper understanding of the whole of biology. It also provides the scientific basis for a brief and well-structured foray into astrobiology (exobiology) - the branch of biology that deals with the possibility, and likely nature, of extraterrestrial life. Astrobiology is currently one of the hottest areas of biological research.

This is all highly relevant to Earth Sciences, because these extremes are where life meets the hard physical constraints and opportunities presented by the Earth's physical systems.

The author explains that although an extreme environment is an area of increased abiotic stress (physical factors such as temperature, pH and salinity), it is also an area of decreased biotic stress (predation, grazing, competition, parasites and diseases). Therefore, when evolutionary adaptations eventually overcome the abiotic stresses, this opens up an area of reduced biotic stress, and consequent opportunities. Therefore, life continually pushes out into extreme environments that were previously inaccessible, and maximises its exploitation of them.

On this basis, the book concludes with a re-telling of the 4 billion year history of life on Earth as the evolution of successive adaptations to colonise extreme environments, and conquering them so that they became part of the mainstream - from anaerobic to aerobic, from ocean surface waters to the full depth of the ocean, and then out onto the land surface, and into every part of it, and up into the air above. This is helpful for understanding the relationships between Earth and Life, and for interpreting the consequent geological record.

John Brenner, MA Cantab, continuing OU Earth Sciences student

with very large but very few veins occur alongside the broad-bladed *Ginkgo adiantoides* form with very small, very numerous veins (Figures 3e & f).

There are lots of unanswered questions with the Ginkgoes and my last question is posed by a very dissected leaf from the Palaeocene of Argentina (Figure 4). Here is proof of the presence of Ginkgoes in South America after the K/T boundary, and I have seen a reference in the literature to *Ginkgo* occurring in the Eocene of Tasmania as well. There is an untold story of the survival of *Ginkgo* in the Gondwanan fragments of the Southern Hemisphere in the Early Tertiary period. I would love to know more about that!

La catastrophe: Mount Pelée and the destruction of Saint-Pierre, Martinique by Alwyn Scarth, 2002, Terra Publishing, 246pp, £19.95 hardback, ISBN 1903544114.

On 8 May 1902 Mount Pelée on the French colonial island of Martinique erupted. Something like 27,000 people lost their lives and the city of Saint-Pierre was annihilated by a devastating nuée ardente. Alwyn Scarth recounts that there had been a violent eruption in AD1300 but this was before the French had settled on the island and although there had been small eruptions in the eighteenth and nineteenth centuries for most of the inhabitants the mountain was somewhere to go for a day out and walking up to the summit became a social outing. Even when two new fumeroles were seen on 4 June 1900 no-one seemed unduly alarmed.

On 22 and 23 April 1902 there were small earthquakes and a rockslide on the sea floor north-west of Mount Pelée cut telegraph cables and so begins the story of what was to become a devastating eruption. We learn of the first ash and dust fall on Saint-Pierre, the destruction of a sugar and rum complex by a mudflow, a tsunami which followed the sudden arrival of masses of mud in the Bay of Saint-Pierre, the growing fear among the residents and then the horror of the nuée ardente.

This is a human story and the author uses extracts from original sources, memoirs and letters written by people who were there. There is a very poignant letter from a businessman in Saint-Pierre to his wife: he had taken her and their children to the south of the island and wrote to her during the night of 7-8 May and posted it in time for it to go on the 6 am departure of a ship. One of the miracles of the catastrophe was that the nuée killed everyone in Saint-Pierre except for two men, one of them being in solitary confinement at the time of the eruption and not found until 11 May. Alwyn Scarth devotes a short chapter to this amazing story.

As well as being of great interest to geologists, because the 1902 eruption of Mount Pelée is one of the 'classics', this is a book which is of general interest: the author puts the story into its economic, social and political setting - in fact, there was an election on 27 April. My non-geologist brother-in-law could hardly put the book down when he was staying for a weekend and kept talking about the awesome power of the nuée ardente.

There are many black and white photographs, some taken before the eruption and some just after, including one of "a small nuée ardente erupted on 16 December 1902" - the much larger one on 8 May must have been truly terrifying. At £19.95 in hardback this is a book to buy.

Elizabeth Maddocks BA (Open)

OUGS field trip to Iceland 1995; Leader: Dr Sandy Smith

Chris Austick, Jenny Bennett, Joan Densham, Jenny Forrest, Peter Franklin, Penny Johnson, Sev Kender, David Maddocks, Elizabeth Maddocks, Jo Marsden, Linda McArdell, Roy Partington, John & Ros Peirson, Joan Taylor & Irvine Walker.
Sketches by Ros Peirson

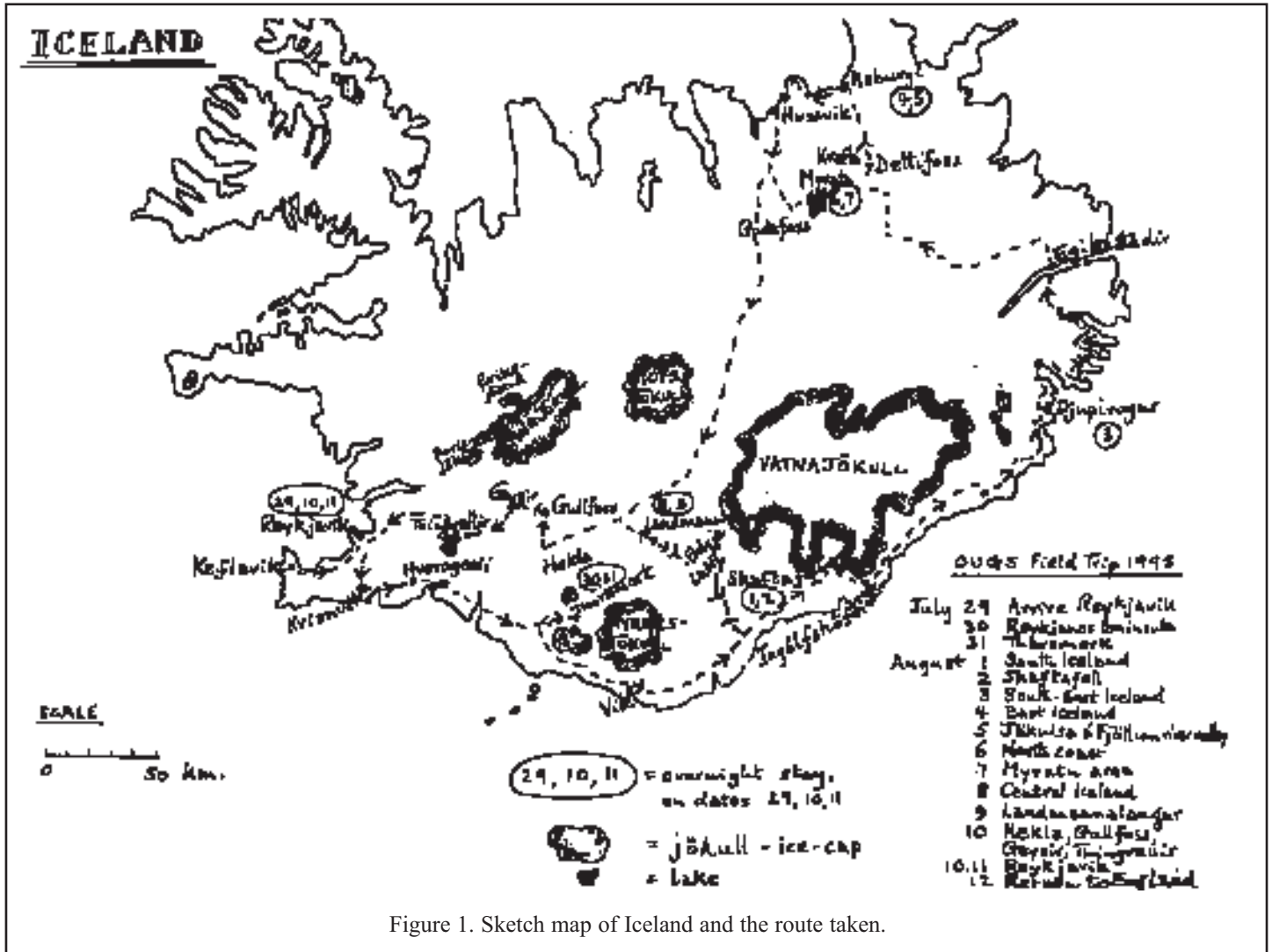


Figure 1. Sketch map of Iceland and the route taken.

This is a compilation of all the reports that people on the trip wrote; we have concentrated mainly on the geology, but there was also plenty of birdlife and flora to see. The drawings are by Ros Peirson; we all enjoyed seeing her sketches through the trip, so I have included several of these. I suppose many of the memories of a trip like this come from the people, and I expect we each have our own, but I still chuckle at some of the things our Icelandic friends said and did. Helgi, Brynnhildur and Brjánn were a great advert for their country! And I remember the odd moments like Joan T and Peter spending vast amounts of money to see some really old rock in Greenland; mass Icelandic sweater buys; riding Icelandic ponies which meant that the wildlife did not fly off; Chris saying he had ridden once before on a donkey at Blackpool; Brjánn putting up "P"-tarmigan for us; the expressions on your faces when we saw something particularly magical; Sandy stopping a sentence in mid-flow because she thought she had seen a gyrfalcon, and then carrying on as though nothing had happened;

Penny realising that neither of us had an alarm-clock, suggesting that we left the blind up so that the light woke us... yes, took us a while, that one! Oh dear, you were all such good company - and the accommodation! The 'girls room' at Hof was much more lively than the men's - amongst other things all the ladies decided to cheer when I actually got my walking breeches done up. (And Jo still spoke to me even after I nearly took over her sleeping mat as well as my own!) Anyway, I am sorry it has taken so long, but here is the story in your own words!

Jenny Bennett

Sunday 30th July

Day 1 was a bit of a 'Cook's Tour', giving us a taster of the kinds of things we would be seeing during the rest of the trip, and 'getting our eyes in' for different types of volcanic rocks. Our first stop was at Kleifarvatn, a lake occupying part of a rift valley that makes up a set of parallel ridges and valleys formed by the overlapping spreading centres that are the continuation of the

Reykjanes spreading ridge. Sandy took this opportunity to remind us of the different types of volcanoclastic rocks: pyroclastics, which have been explosively erupted into air, and hyaloclastites which have been erupted beneath ice and shattered by contact with the ice.

We stopped again at Krísuvík to see the hot springs. An impressive jet of steam was continuously erupting from a hole which had been drilled to pipe the hot water out. The pipes have been removed but the hole makes an impressive display of steam. Hot water was bubbling up at various other places around the main jet giving off a strong smell of sulphur. The water in these hot springs is meteoric: rainwater and streams percolate downwards and are heated. The hot water dissolves various minerals, which are precipitated when the water cools on reaching the surface.

Stop 3 was for birdwatchers. The cliffs at Krísuvíkurborg are made of alternating lava flows and pyroclastics, and kittiwakes and a few guillemots nest on the ledges formed between the different layers.

After lunch we climbed Eldborg, a small cone formed by a classic composite volcano. A dip in the crater wall showed where the lava from the last eruption had flowed out of the crater. The lava channel could be seen running down the side of the cone and across the road towards the sea.



Figure 2. the Raufarhólshellir lava tube.

The next locality was impressive once we found it! Sandy and Brjánn (our guide) wandered around the rough ground beside the road while the rest of us sat in comfort on the bus. They did eventually find the entrance to the Raufarhólshellir lava tube (Figure 2). We had to scramble down some loose blocks, and found ourselves at one end of a tunnel about 6 or 7m in diameter. The tube was formed as the edges of a fast moving lava flow cooled, became more viscous and solidified, leaving the lava flowing down the centre. According to the guidebook we should have been able to see lavatites - the lava equivalent of stalactites, but we could not find any.

The last adventure of the day was driving up the valley of the Markarfljót river - a classic example of a braided river valley, fed by three ice-caps. We stopped to look at Gígjökull, a glacier extending down into the valley, but our desire to shelter from the rain exceeded our wish to listen to Sandy's words of wisdom, so we all ran for the bus. The driver then proceeded to drive through



Figure 3. Crossing the river with Helgi, our driver.

the outflow river which we had all assumed was impassable, with the water lapping under the door. We stopped to make sure there was no water in the luggage compartments. We did this again, but before the final crossing Helgi (the driver, Figure 3) decided to put all the luggage and sleeping bags inside the coach! However, we reached our accommodation safely, ate a large supper, and after negotiating the route to the outside bathroom and 'bagging' a sleeping space, we all turned in for the night. We then all discovered who snored and who did not!

Penny Johnson

Monday 31st July

A walking day, so we left Thórsmörk and crossed a classic and constantly changing braided stream (it was full of glacial melt water with a high bed load and coarse sediment) so we were able to appreciate what we had driven over the night before. We



Figure 4. Stakkholtsgjá.

walked past ignimbrites (welded tuff) and hyaloclastite and crossed a series of increasingly wide rivulets - mere rehearsals for the final one which was wide, fast flowing and knee deep if you slipped off a stone! Brjánn, our Icelandic guide, chivalrously stood in the middle and handed us across. Some were awarded the 2-dry-feet award, some the one-dry-foot consolation prize and some of us did not get a prize at all.

We walked up a wide valley with cliffs of cross-bedded hyaloclastite, some were porphyritic and perhaps had fallen from higher up the canyon (Figure 4). Our coffee break was beneath high cliffs with circling fulmars, in a deep valley (over 30m). Possibly a fault had been exploited by the glacial river which had easily eroded the friable hyaloclastite cliffs; this was definitely not a glacial canyon, the sides were too steep and there was no overhang. We could see 'flutes', perhaps part of a pot hole where surface streams had entered and mini canyons where side streams had joined. We walked between narrowing canyon walls hung with velvety olive green moss to the pot hole down which the river crashed. We returned down the canyon and across the river with different people gaining the dry-foot awards.

After lunch we walked up another canyon on a pillow hunt. We think we found some with signs of chilled rind, perhaps they had tumbled down slope into the hyaloclastite or had been formed under water or ice. We continued climbing but were distracted by views of glaciers (jökulls) with their long waterfall tails and dust encrusted overflow slumps.

Some of us continued the climb to the top of the peak, from where we viewed a panorama of the mountains, our little red roofed mountain hut and its braided river barrier. We walked back through a dwarf birch forest from which sheep have been excluded to allow the trees to regenerate. Continued back to Thórsmörk along the valley floor, taking quite respectable little streams in our experienced stride. A most interesting day with only a hint of drizzle to make us appreciate the dry weather that followed.

Joan Densham

Tuesday 1st August

After leaving the Thórsmörk valley we drove to Seljalandsfoss

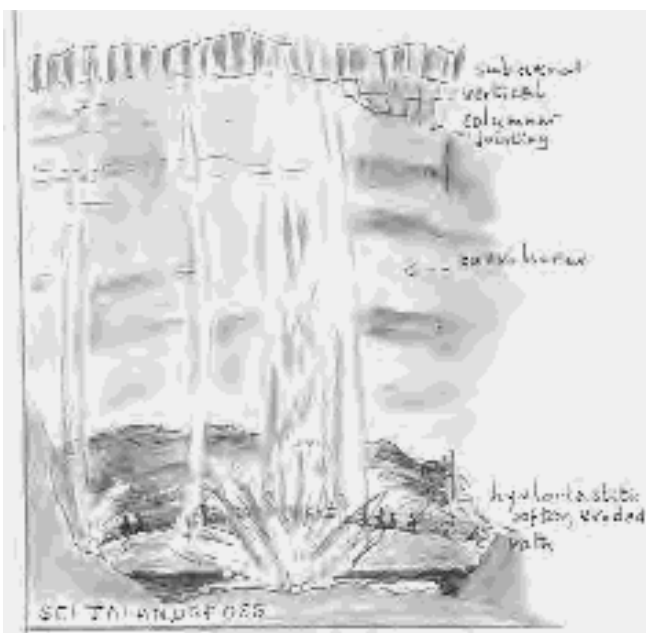


Figure 5. Seljalandsfoss.

(Figure 5) where water falls 60m over the former sea cliff. The lower 10m or so of the cliff is formed of hyaloclastite and above this are subaerial basaltic lava flows. The lower 2m show well-defined columnar jointing and the higher basalts can be divided into two flows. The water falls from the junction between these over curvilinearly jointed basalt. Above the falls and to one side the topmost basalt is approximately 12m thick and is more regularly fan vaulted.



Figure 6. Rootless craters at Herjólfsstadir; Brjánn running to look for cut-away crater in Eldhraun (lava came from Eldgjá 934 AD).

After a brief stop at Skógafoss, a fall over the same sea cliff, the road crossed Myrdalssandur, a vast black sand outwash plain from Myrdalsjökull. The sandur was dotted with cones of varying height, from approximately 2 to 6m. These are rootless craters showing no internal structure which are formed when lava flows into a lake or mud, trapping water which changes to steam and erupts explosively (Figure 6). The cones are formed of very shattered twisted pieces of lava. These cones were formed during the Eldgjá eruptions of around 934 AD.

A very long drive over a barren area crossed by many rivers led to the top of the eastern rift of the Mid Atlantic ridge. Looking across approximately 15km of apallhraun (aa lava) towards the western rift, a series of cones are visible. They are light grey with reddish tops. Crossing the lava, we climbed Laki, an 818m hyaloclastite mountain (Figure 7). About halfway up is a collapsed lava



Figure 7. Laki mountain and crater on Laki fissure.

tube about 8m wide. From the top the cones, together with fissures, are seen to be in a line trending NE/SW (040°) that cuts straight through the mountain and runs roughly equidistant from the east and west rifts. The cones and fissures lie in a graben feature bounded by the east and west rifts. These cones are the result of a catastrophic fissure eruption in 1783-84, which covered 556km², the greatest effusion of lava in historic times. The fumes of fluorine and sulphur dioxide caused livestock to die and farmland to be contaminated. One fifth of the human population died from the resulting famine.

Examination of a cinder cone showed it to be composed of scoria and spatter. There are lava tubes running from the crater, one of which was large enough to enter. There are 'stalactites' of lava, indicating a flow fast enough to leave the roof of the tube dripping.

The return journey was made by the same route to the accommodation at Hof.

Jenny Forrest & Irvine Walker

Wednesday 2nd August



Figure 8. Skaftafellsjökull; the rocky outcrop on the horizon is Snaebreith 2041m.

After breakfast under canvas in the shadow of a sun-drenched glacier, to the chorus of Redwing, Golden Plover and Wheatear we travelled to Skaftafellsjökull, one of the many glaciers on the southern edge of the largest ice-cap in Europe, Vatnajökull (Figure 8). This glacier has receded some 2km this century allowing ample evidence of parallel ridges formed by terminal moraines which have been dated using geomorphic and lichenometric as well as documentary and photographic evidence. Walking up the nose of the glacier (tricky in rubber-soled boots) enabled observation of the debris carried on the ice surface. Within an area of approximately one square metre it was possible to identify eight different rock types, from basalt fragments to pieces of pahoehoe lava: a subject for a future research project?

One depositional feature, perfect cones of small rock particles, led to the formation of a self-help group which hypothesised that these fragments had originally been carried in the surface water on the glacier, and had been washed through one of the many melt-water holes to be released like the sands in an hourglass. Again more research would be required if funding was available. Over lunch another self-help group formed to explain to our guide the difference between a sill and a lava flow. Evidence of glacial erosion, lateral and medial debris could be seen on other glaciers

in the area while the valley in which we sat showed deep, horizontal striations in the polished rock walls as well as basalt sills (Figure 9). The waterfall Svartifoss allowed close inspection of columnar jointing, chisel marks and plumose structures, all features of differential cooling in the basalt face.



Figure 9. Svinafellsjökull; a basaltic sill jumping a bed.

From a view-point on the walk back to the car park the origins, power and consequences of sub-glacial eruption could be appreciated in the form of a 'sandur', an area of rock boulders and fragments laced with braided streams which stretched westwards to Myrdalsjökull some 120km distant.

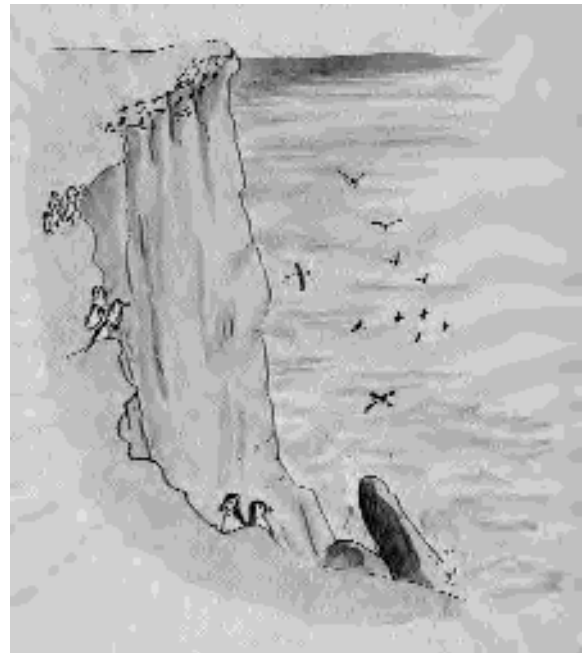


Figure 10. Puffins on Ingolfshöfði Island.

The evening tutorial was conducted by a direct descendant of one of the first settlers who took some of the group across the sandur in a tractor to an outcrop of basic-to-intermediate basalt (Figure 10) where we met Skumur (*Stetorarius skua*), Lundi (*Fratercula*

Peter Franklin

Thursday 3rd August

DEURZEN
Rue KATTAKELER
BERNÉS

Jäkalsörön 24 August 1904

Our first stop was at Jökulsárlón; a glacial frontal lake bounded seawards by terminal moraine and linked to the sea by a river (Figure 11). The lake contained a large number of impressive icebergs, many of which were strikingly patterned with dark stripes of sediment. The icebergs calve as a result of seawater (which is warmer than the lakewater) entering the lake at high tide and undercutting the front of the feeder glacier Breiðamerkurjökull. The icebergs can persist for up to three years before melting sufficiently to escape downriver to the sea. The lake is gradually silting up through the release of sediment from the melting icebergs and glacier front. Some of the group took the opportunity of a boat trip to get closer to the glacier and brought back huge chunks of ice. We left Sandy and a few others birdwatching; to their delight they saw a family of snow bunting - on snow!

Felseninsel
 mit unentwickelter
 Vegetation
 (Felseninsel)
 Algen

Inseln
 mit
 Grasland

Vegetation
 Grün

19. 10. 1965 in S. 1. 1965

Our second stop of the day was a dozen kilometres east of Höfn, which is roughly 100km by road north-east of Jökulsárlán, where a gabbroic intrusion within Tertiary basalts has created the prominent Vesturhorn headland. The gabbro in turn has been intruded by a granitic mass on the landward side. By virtue of the wonderfully clear conditions, the irregular contact between the two intrusions could clearly be seen in the high cliff above the road.



Although it was not possible to examine the contact closely, several blocks were found in the scree at the roadside which gave clues to the relationship between the two intrusions (Figure 13). This was also the day when we found zeolites! Helgi and his son were also enthusiastic spotters for us.

Chris Austick & Jo Marsden

Friday August 4th

A wet start to the day, the first as it happened, but those assigned to the washing up were rewarded by uplifting views of the mountains rising up from the other side of the fjord.

OUGS Journal 23(2)
Symposium Edition 2002

the usual unlimited visibility, the continuation of the dyke could clearly be seen on the opposite side of the Breithdalsvík inlet.

At this point, we diverted northwards for a few kilometres to view the rock and mineral collection in a house and garden in the village of Stöðvarfjörður. This is a wondrous place for geologists. Much 'wowing' and drooling over the minerals, rocks, lovely gardens and plants. The delightful house (we did not need to remove our shoes, but felt that we should!) is also taken over by beautifully and painstakingly arranged collections, all apparently the life work of one elderly lady. As Joan Densham commented 'a salutary warning to rock collectors!' From here, a short backtrack to Heydalir and to continue the safari, up some 600m over Tertiary lavas, pyroclastics and intrusive complexes to the town of Egilsstathir for a bank stop. Much of the journey was on unmetalled roads with hairpin bends. Bang on cue, just as we were negotiating a particularly steep, twisty section, Helgi's phone rang and he continued to drive with one hand whilst taking the call.

Driving west on a 'murrum' road, reminiscent of East Africa we could see the geothermal source of the town's hot water, flocks(?) of roches moutonnées, huge moraines and other glacial deposits (eskers?). In this region are large sheep farms and lovely waterfalls; we stopped for lunch beside one of the falls. Alongside the road, we discovered layers of pumice, fragments of which our excellent and co-operative driver demonstrated could be floated on a convenient stream.

Climbing up Jökuldalsheidi plateau (heidi = heath), we learned how the area had been covered in rhyolitic tephra in the 1875 fissure eruption north of Askja and many farms had become deserted as the occupants emigrated to Manitoba, where spoken Icelandic may still be heard, apparently. We could see clearly the 1833m strato-volcano of Snaefell. Leaving the watering hole at Möthrudalur, we stopped to take in the view of Askja caldera ('Sandy's mountain') in the Dyngjufjöll range, apparently flanked by the oddly symmetrical birthday cake tuya Herthubreith (1682m) and the text book shield volcano Kollótadyngja (1180m). In the 1875 eruption of Askja 2km³ of tephra was ejected which carried as far as mainland Europe.

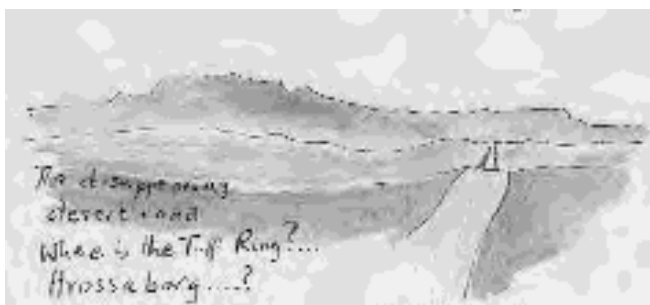


Figure 14. Myvatnsöræfi "The Wilderness of Myvatn". The disappearing road. Where is the Tuff Ring?.. Where is Hrossaborg?

Following Highway 1 for another 40km from Möðrudalur (Figure 14), we were able to drive along a short track right into the tuff ring of Hrossaborg (Figure 15). This is a huge amphitheatre-like structure of outwardly sloping tephra. We climbed the rim to examine the fragments of accretionary tephra and to admire the view. The next major stop before reaching our very comfortable hostel type accommodation at Skulagarthur (showers, waitress service, no

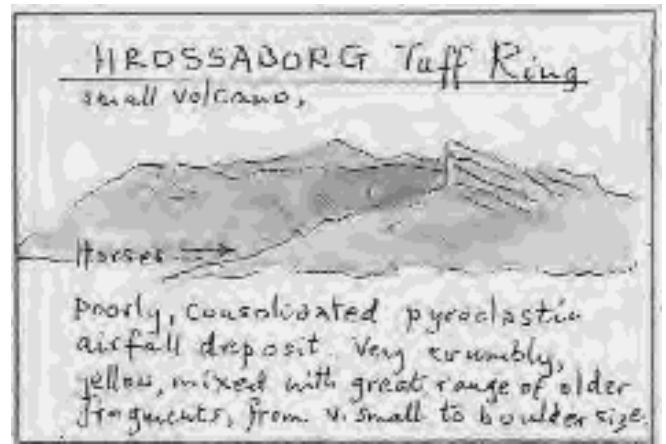


Figure 15. Tuff Ring.

washing-up, excellent meals including a surfeit of fresh salmon) was at the stupendous Dettifoss waterfall. This has the greatest volume of any waterfall in Europe. As we stood, stunned by the sheer power, noise and vibration of that vast quantity of water in motion, it was good to know we would revisit this awesome place tomorrow.

Roy Partington

Saturday 5th August

As we left our overnight stop at Skulagarthur we were able to see to the north the enormous sandur (outwash plain) covering about 200km² deposited by the Jökulsá River. We stopped briefly to examine some fissures up to 3m wide and all aligned NNE/SSW, corresponding to the tectonic trends in this part of the island. They became active in 1975 when the volcano Krafla, 40km to the south, showed signs of awakening. The activity ceased in 1984 when Krafla finally erupted.

The main feature of the Jökulsárgljúfur National Park is the 30km long canyon carved by the Jökulsá River (Figure 16).



Figure 16. Canyon below Dettifoss looking north from east bank.

At the head of the canyon is Dettifoss, the most powerful waterfall in Europe (Figure 17). The 44m drop was taking about 500m³s⁻¹ of grey glacial melt water at the time of our visit. It has been calculated that the immediate post-glacial flow was around similar to the Amazon today at 500,000m³s⁻¹. The exposed stratigraphy by the falls showed Pleistocene inter-glacial lavas, interspersed with tillites, topped off with a 6-10m thick post-glacial lava.

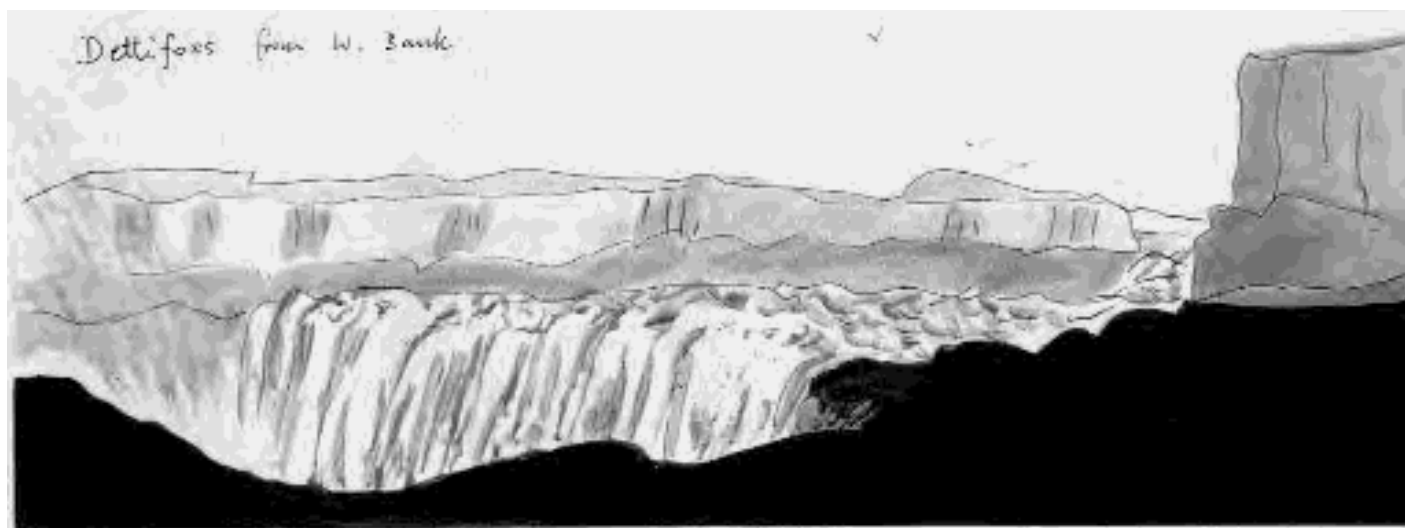


Figure 17. Dettifoss - the most powerful waterfall in Europe.

We walked about 8km of the canyon from Hólmatungur to Vesturdalur looking at, among other things, the spectacular columnar jointed basalts. In some flows the jointing was vertical, in others, the basalts had erupted beneath tephra, the irregular cooling surface giving rise to beautifully curved columns. We saw many strange formations, including some which Brjánn assured us were trolls.



Figure 18. The horseshoe -shaped canyon of Ásbyrgi.

Our final visit was to the now dry horseshoe-shaped canyon of Ásbyrgi (Figure 18). At its head are the remnants of a major waterfall and a large dry river channel. It carried Jökulsá water until about 2500 years ago. A quick calculation shows that about 0.25km³ of basalt has been removed, mainly in the immediate post-glacial period. Truly, a testament to the massive eroding power of a big river carrying large quantities of sediment.

David Maddocks

Sunday 6th August

We left Skulagarthur on the north coast at the edge of the sandur of the Jökulsá (where we had been most comfortable, even though some people had been disappointed to find that the large notice saying INN meant IN and not INN) and drove past a large geot-



Figure 19. Farmer Priest's house.

hermally heated fish farm and on round the Tjörnes peninsula. From the high coast road we could see the island of Grímsey, the northern end of which is just inside the Arctic Circle (which incidentally runs down the middle of the priest's bed so that he and his wife find

themselves one in the Arctic and one not (Figure 19)). As we rounded the north end of Tjörnes we suddenly had a splendid view of the snow covered Tertiary volcanic mountains to the west. (We passed the island, which was the home of Einar Benediktsson, who nearly managed to sell the Aurora Borealis to an English business man). We then came down a major transform fault, marking the southern edge of the transform fault zone, into the pleasant little fishing town of Húsavík.

We drove up the valley of the Laxá river, which flows out of Lake Myvatn and has water sparklingly clearer than the glacially fed Jökulsá. On the way we enjoyed a bird stop to watch Harlequins, a Whooper Swan and other birds. To increase the appetite for lunch we skipped up Vindbelgjafjall, a thousand foot 'hill', from the top of which we had a marvellous view in all directions of the Myvatn area.

After lunch we drove round the lake, seeing many birds on the way (Scaup, Merlin, Redshank, Whooper Swans, Red-throated Divers, Mergansers among others) and explored the area of boiling mud pools of Namaskard. The formation of these pools, one of which was found to have a pH of 4 is of course due to the high geothermal gradient of the area (perhaps 200-300°C km⁻¹ compared with the usual value of about 20-30°C km⁻¹). Nobody took an involuntary mud bath though we were warned to keep to the marked paths since the crust is so thin in places that one might go through and start a new pool.



Figure 20. Viti in Krafla Caldera.



Figure 21. Panorama from Vindbelgjarfjall over Myvatn.

We then made our way towards Krafla via the geothermally driven power station. It was remarkable to see steam coming up from shafts driven into the ground just next to some areas of snow. Driving shafts into the ground in such an area is somewhat hazardous; in one case what came up was not steam, but lava!

Finally we walked up to the area of the 1984 fissure eruption of Krafla. The original shield volcano was about 25km across. The underlying magma chamber, 3km down, produced these as well as the magnificent pyroclastic crater of Viti (1724) and the line of the small craters along the 1984 fissure one of which we visited (Figure 20). We found magnificently fresh lava flows, with many examples of pahoehoe forms and in some places considerable deposits of sulphur crystals. The whole scene was made even more astonishing by the steam and sulphurous fumes which wafted about, giving the superficial impression that the eruption had only just happened! We made our way back to comparative safety (the underlying magma chamber is inflating at the moment) over lava flows with north-south trending fissures, which we stepped over with some care, and arrived at Reykjahllith on Lake Myvatn (Figure 22).

John & Ros Peirson



Figure 22. Church at Reykjahlith, Myvatn.

Monday 7th August

The day started with a visit to Skútustathir (named after a local warrior, Skuta) along the central part of the southern shore of Lake Myvatn. The area is noted for rootless or 'pseudo-craters' which were formed about 2600 years ago when lava from Threnslaborgir (some 12km to the east) advanced across existing wetlands. The heat from the lava turned the trapped water into superheated steam which then exploded through the overlying lavas producing cinder cones. The most prominent craters are thought to have formed over freshwater springs, where the continuous supply of cold water enabled some of the craters to develop to 8-11m high. In appearance, the individual pseudo-craters

resembled the real scoria craters seen on previous days. One characteristic was evident, these pseudo-craters were distributed over a wide area (the former wetland) unlike the linear distribution of the fissure-generated craters.

A short drive away on the eastern side of Lake Myvatn, at Dimmuborgir, we walked through the remains of a classic drained lava lake. The lake was created some 2000 years ago when a dam formed, trapping lava from a fissure eruption from the Lúdentiborgir-Threndlaborgir crater row (to the east). It was about 2km across, and a shield-like dome of cold lava formed over the lava lake. Where channels of steam and gases rose, patches of lava were solidified. Eventually the lake drained, probably over several days, and left lava as pillars, many over 10m high; these now bear 'tide marks' from pauses in the draining of the lava and scratch marks as the overlying roof collapsed. Today the landscape is reminiscent of a wild, almost baroque rock garden with pillars, arches and wild shapes of scoria overgrown with birch trees and a multitude of wild flowers.

The extent of the former lava lake was viewed from the top of the Hverfjall fissure volcano to the north-east of Dimmuborgir (Figure 21). This huge crater formed from a series of sub-aerial explosive events 2500-2700 years ago. Much of the material seen was fist-sized tephra, but the slopes were littered with large blocks of pre-existing solid lava. This classic tephra ring dominates the surroundings: it stands 160m above the surrounding land, is 1200m wide at the rim and 3000m at its base. From the top there are splendid views across Lake Myvatn.

Joan Tavlör & Linda McArdell

Tuesday 8th August

There was a dampening start to the day. We awoke to the first proper rain since our first day in Keflavík, and it was a long walk to the breakfast tent. We left Lake Myvatn and its ‘midgets’ (our Icelandic guide’s word for ‘midges’) after breakfast and drove about 48km north-west to Godafoss waterfall (Figure 23); it had stopped raining.

In my opinion this waterfall is the most striking and scenic that we had seen so far. Historically it is the location where in 1000 AD pagan idols were thrown into the river, symbolising Iceland's adoption of the Christian faith. There are two falls separated by lava columns, which mark the border between Tertiary and Pleistocene rocks where a fault was probably exploited and widened by the river. The basalt is very thick and is probably a solidified lava lake.



Figure 23. Godafoss.

Our next stop was about 40km southwards at Aldeyrfoss waterfall, following the valley of the river Skjálfandafljót and passing the southernmost farm in this area. The rock formations are dazzling. The straight basalt columns at the bottom of the falls are adorned by a cover of the most extravagantly twisted and curved column fans that I have ever seen.

After Aldeyrfoss we embarked on a seven and a half hour long journey of about 240km south-west through the central highlands between the icecaps Hofsjökull and Vatnajökull, a bleak and barren region. The coach radio was playing Icelandic music which some of us felt did not add to the character of the wilderness around us. After some diplomatic negotiating it was turned off. The track deteriorated and became slow and bumpy as it turned and twisted its way through the region. Although there was very little traffic (one vehicle or so per hour) we did pass several cyclists! We forded about 35 streams (Figure 24), and one particular braided stream had actually captured a significant section of the track with one of its channels, forcing our driver to stop for a while in order to work out a safe route.

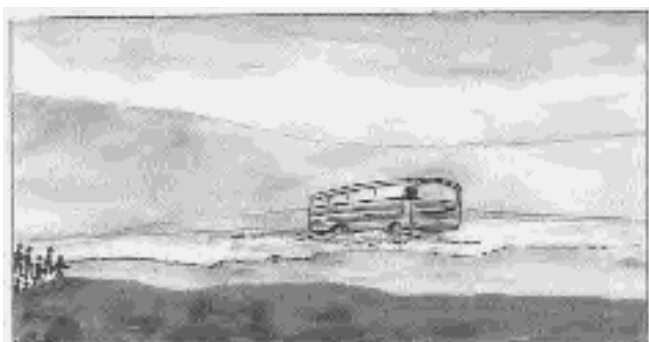


Figure 24. Uncharted road - our bus fords another braided stream ... we all had to get out first!.

A vast grey wilderness of rubble and undulating terrain ensued. Rocks of various sizes litter the glacial landscape which reflects tephra horizons from different eruptions. Many small areas of snow that have not thawed dot the panorama in places. The plant life is meagre, small flowering plants and moss surviving sporadically in sheltered crevices between the strewn rocks and on the banks of the streams. I saw no animal life - bird kind included.

We stopped for 10 minutes during the course of our journey to look for the subglacial outcrops of rocks called roches mouton-

nées. We discovered a few, and, after examining their shapes and scratched striations, came to the conclusion that the flow of ice was approximately NE (035°).

Curious landmarks were the very frequent small lakes present in localised depressions with no streams entering or leaving them. The conditions are periglacial, and permafrost is only about one metre below the surface, hence forming these periglacial 'swamps'.

There were two events which have stayed in my mind. During the late afternoon we made a so-called 'Japanese photo-stop' at a locality where a little stream valley was immersed in the flowers called Arctic River Beauty. The valley was filled with a splendid light magenta bloom and our cameras were snapping. The second was a rather unusual incident. At about 5.40pm five unshaven men stood across the track ahead of us and stopped the coach. They remonstrated fairly intensely with our guide and I think there was some initial anxiety in the coach. They were asking rather persistently for a lift and it took our guide several minutes to persuade them that this was not going to happen. It transpired that they had hiked to the track from the interior where they had been camping for several days, but had now missed their bus (apparently the occasional public transport coach does journey through these parts during the course of the week).

At 6.30 p.m. we arrived at a hostel called 'Hrauneyjar Ferðastax' where we were to stay for the following two nights. To our delight the accommodation was unexpectedly good, some of us even enjoying single rooms.

Sev Kender

Wednesday 9th August

This was another misty day and we set off into the Landmannalauger area (Figure 25). The whole of this area is dominated by Hekla and it is the largest rhyolitic area in Iceland. There are large amounts of acid tephra and the scenery is eerie, with volcanic cones which have been thermally weathered, resulting in amazing soft colours, greeny yellows, soft reds, browns and then the vivid green of mosses. We stopped to look at the Eldgjá fissure; visibility was very poor but we could see that there was a large volume of lava with tephra on top. There was also some third stage tephra from the small spatter cones on the surface of the fissure. The Eldgjá fissure trends SW/NE, parallel to the Laki fissure seen in the early stages of our trip. Looking at the rock types visible we found rhyolite, showing us that the material here is indeed enriched in silica. We also found hyaloclastites and some pillow lavas visible at the roadside. However, visibility really was very bad so we went on to Laugahraun.



Figure 25. Rhyolite mountains in Landmannalauger.

This apparently was one of the places where we might have stayed, a very basic mountain hut, but one which had its own hot spring feeding a bathing pool at the foot of a lava flow. Sandy assured us that this is quite an experience late at night. We walked along the lava flow here, or rather, clambered over and through bits of it! This was one of the places where decent boots are essential as the flow is mixed rhyolite and basalt with sharp pieces of pitchstone and obsidian. Beautiful flow-banding in the lava was visible, some showing red and black flows. We also found a rhyolitic dyke with obsidian and pitchstone in the middle. Sandy explained to us that pitchstone is in fact hydrated obsidian (and the obsidian is much sharper!). There were chilled margins to this dyke and some of us were sure we could see rhyolitic pillows in the area. The top of the lava flow is aa lava and rhyolitic. This means that the blocks are enormous, boulder sized, which makes the terrain very difficult indeed. We followed a stream alongside the lava flow; the stream had evidently made its course through the much softer glacial material. We reached Brennisteinsalda at the top of the fissure which apparently opened in the sixteenth century. Here we saw sulphurous hot springs and fumaroles: these were active and hot, it was possible to see delicate sulphur crystals at the edges. We made our way back down to the mountain hut for lunch, looking across to the crater at Northurnámshraun. There we saw that the rhyolite and basalt were mixed, the flows were much less thick, presumably as the flow would have been much less viscous. Joan Taylor found 2cm-long blebs of basalt in the pitchstone, again showing the mixing of material.

After lunch, we went down to the hot spring area, all very basic, and with the driving rain and nowhere to change, I am afraid my sense of adventure left me! Several hardy souls went in though and appeared to enjoy it. The scenery was extraordinary, a weird juxtaposition of steaming volcanic cones, a glacier and outdoor swimming.

Our final stop was at Northurnámshraun, where we looked at the explosion crater. We were further in to the fissure here, and could see that the material erupted was mainly basalt. Along the road towards Ljótípollur (the 'ugly puddle'!) we could see that the material used in the wall along the road was also basaltic cinders. We made our way back to the hostel where anyone who had any whisky left was very popular and explained some idiomatic English expressions to our Icelandic guide. He was particularly taken with the phrase 'tired and emotional' once he had understood; it took a fair bit of explaining!

Jenny Bennett

Thursday 10th August

This was our last day in the field. Unfortunately the visibility was poor and we caught only glimpses of the lower snow-covered slopes of Hekla as we journeyed west. However we did see evidence of the light-coloured pumice and ash from the eruptions of this 1491m active volcano.

Hekla is a central volcano with its own magma chamber and forms a 6km ridge with a fissure crater row aligned ENE/WSW along its whole length. Its first recorded eruption was in 1104 and since then it has erupted at intervals of from 10 to 120 years, the last eruption being in 1991. The greater the repose time between eruptions, the more silicic are the first products of the activity as there has been more time for differentiation in the magma chamber. Later stages of the eruption produce mainly basaltic andesites (Icelandite).

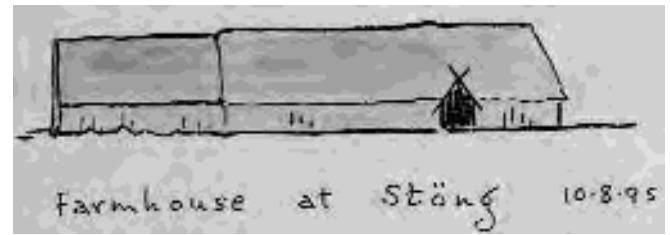


Figure 26. Farmhouse at Stöng.

Our journey took us by the River Thjórsá, the longest river in Iceland (230km): it is mainly glacial water plus some fresh water. The once prosperous farmland of the Thjórsárdalur Valley was covered by pumice during the 1104 eruption and 20 farms were destroyed. A farmhouse at Stöng has been excavated (Figure 26); it was only partly buried and was well preserved. The ruins have been roofed over and we were able to get the feel of 12th century living conditions. It is likely that 50 to 100 people lived in this farmhouse which would have been built of wood, stone and turf. It was heated by a fireplace running the length of the main living area.

Before reaching Stöng we had a short stop to see the picturesque little waterfall of Gjáanfoss, a set of waterfalls in a canyon fed by spring water. Columnar jointed basalt was overlain by confused columns with ash or a hyaloclastite deposit on top; from our viewpoint it was not possible to decide which. A vertical displacement in the basalt columns seemed to indicate a fault.



Figure 27. Hjólparfoss.

After Stöng there was yet another foss to see, this time Hjólparfoss in the River Fossa (Figure 27). A confusion of basalt columns indicated the different cooling periods, the curved columns probably a function of slow deformation before the lava set solid.

Our next stop was to see the spectacular 'Golden Falls' of Gullfoss (Figure 28). Unfortunately it was drizzling and windy so we did not see the falls at their best. Gullfoss is two falls (glacier fed), the total height being 32m with the lower fall at 21m. The falls are controlled by two sets of faults, one running NNE/SSW (the regional rift trend) and the other NE/SW. The recession gorge, i.e. the gorge downstream of the falls, is 2.5km long. The average discharge is $118\text{m}^3\text{s}^{-1}$ and the sight and sound of the water thundering down into the gorge 32m below was quite spectacular. The upper fall has two lips made up from two basalt lava flows while the lower fall has just one. The hard basalt of the upper fall



Figure 28. Gullfoss.

protects the more easily eroded underlying rocks: two beds of cross-bedded sandstone separated by a bed of frost-disturbed siltstone and, overlying the basalt of the lower fall, a layer of tillite.

Our next spectacle was at the Geysir field to see the hot springs. The long axis of the 6 by 0.5km field runs NNE/SSW, parallel with the prevailing tectonic direction in the region. Geysir itself is the world's largest erupter (or spouter) and gave its name to the phenomenon we had come to see (Figure 29). At present the only active geysir here is Strokkur but it put on a fine display for us. After bubbling and subsiding for several minutes a dome of water grew and then erupted into a great fountain which can be up to 40m in height. Around the edges of the geysirs is siliceous sinter thrown out from the erupting steam vent.

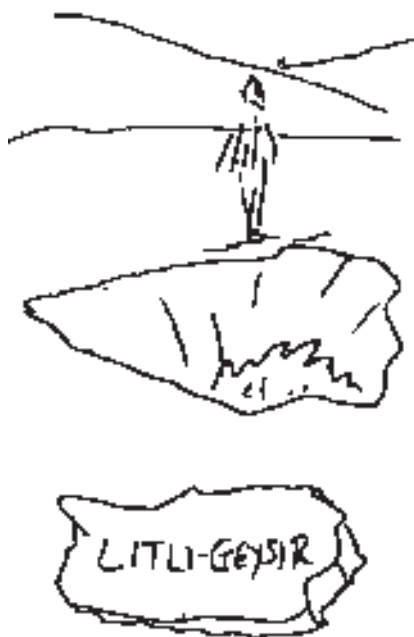


Figure 29. Preliminary sketch of Litli Geysir.

The high geothermal gradient in this area results in meteoric water in cavities just below the surface being superheated. The reduction of pressure on the heated water as water vapour foams and overflows at the surface results in the vast volume of spray surging up.

Our final stop was at Thingvellir where from 930 to 1800 AD the old Icelandic Parliament, the Althing, met (Figure 30). They could not have chosen a more impressive site, for here is the summit graben of the Mid-Atlantic Ridge. The ridge is displaced eastwards by four sets of *en-echelon* faults running NNE/SSW and the total width of the graben between the outermost faults is about 5km.



Figure 30. The Alþingi at Thingvellir.

As we approached the western side we estimated the downthrow of the largest fault, Almannagjá, as 30 to 40m to the east; on the eastern side of the rift the downthrow is to the west. We walked beside the towering basalt wall of Almannagjá and up on to the American Plate (Figure 31). From here we looked across the rift towards the Eurasian Plate; the rift is largely filled with water forming the deep Lake Thingvallavatn.



Figure 31. Members of the OUGS near Alþingi.

There has been no volcanic activity here for 2000 years but it is a region of tectonic activity and it was a great thrill to realise we were actually standing on that part of the Mid-Atlantic Ridge which is on land. What more fitting end could there be to our last day in the field in Iceland.

Elizabeth Maddocks

Acknowledgements

Ros Peirson has kindly given permission for her paintings to be reproduced here. Her initial sketches are done in pencil, inked in later and completed with a watercolour wash. Regrettably they cannot be reproduced here in colour.



Figure 32. Snyrting (Icelandic loo).

Book reviews

Mantle Convection in the Earth and Planets by Gerald Schubert, Donald L Turcotte, Peter Olsen 2001, Cambridge University Press, 940pp, £49.95 (paperback) ISBN 0521798361 (£140.00 (hardback) ISBN 052135367X).

Mantle convection is the most important process in the mantle and influences many aspects of Earth and planetary sciences. This book is intended as a research monograph and a comprehensive synthesis of all aspects of mantle convection in the Earth, terrestrial planets, the Moon and the Galilean satellites of Jupiter. The authors' intention was to provide a thorough treatment of the subject appropriate for anyone familiar with the physical sciences; therefore some parts of the book are heavy on maths.

The book begins with the historical background before proceeding with tectonics, the Earth's structure, mantle temperature, thermodynamic properties and viscosity. Following this reasonably descriptive beginning, the authors then provide a useful chapter on basic equations that leads to the more mathematical parts. My own maths expertise is weak but this does not detract from the book, as the difficult maths may be skipped over. Having set the scene and provided the tools, the authors take us through the physics of mantle convection, geochemical observations and chemical geodynamics before discussing the thermal history of the Earth. Throughout the book, the authors highlight questions - to focus the discussion and suggest avenues of future research. The questions are presented as in-text questions and summarized in the final chapter where definitive answers are provided to some and the more controversial and far-reaching are addressed.

This book is the best-compiled text that I have seen and may be used as a reference work for researchers in the many fields of Earth and planetary sciences. The reference list extends to 76 pages and is further backed up by an author index that is cross-referred to both the text and the reference list; an appendix of the variables from the equations is also cross-referenced to both the equation number and page; the comprehensive subject index is equally accurate and easily used. There are numerous black and white illustrations, many of which are repeated in colour. I worked my way through the book more than once and found that my lack of maths was no handicap. Much of the information is familiar but there is also up-to-date discussion of the latest research developments in the science. On a personal note it was interesting to come across Wadati for the first time since S102. With its broad subject matter this book can be thoroughly recommended to Earth and planetary scientists at any level.

Mike Hermolle, BSc(Hons) NatSci (Open)

Photographic Guide to Minerals of the World by Ole Johnsen, 2002, Oxford University Press, 439 pp, £17.99 (hardback) ISBN 0198515685. Out of 4,000 minerals known at the time of writing, about 500 are described in detail in this beautifully illustrated book. Drawings or excellent colour photographs illustrate nearly all the minerals described. All but five of the photographed specimens belong to the Mineral Collection of the Geological Museum, University of Copenhagen. The author has written about minerals and their properties that can be seen with the naked eye or with a hand lens so topics such as crystal optics and X-ray crystallography have not been included.

The book is divided into two main parts, Part I deals with Mineralogy and Crystallography while the larger Part II is the comprehensive guide to the minerals. There is also Part III which contains useful tables of common minerals and their properties, the Periodic Table and symbols and atomic numbers of selected elements. A glossary explains any technical terms not covered in the introductory sections and there is also a complete index.

Part I explains how to study minerals and provides a basic introduction to crystallography. In the first section the author defines "What is a mineral?". He briefly describes how, why and where minerals occur and explains how mineral names were derived - from old mining terms, according to a typical property, from its chemical composition, after a type locality or after the name of an individual.

Sixty pages are devoted to crystallography and although some knowledge of crystallography is required for anyone interested in minerals, there is probably more detail in the sections about crystal systems than the amateur requires. However, the sections on formation and growth of crystals, and the chemical, physical and optical properties of crystals are clear and understandable by the non-specialist.

The mineral descriptions in Part II are divided into native elements, sulphides, halides, and oxides and hydroxides, each one starting with a general explanation. Descriptions include the mineral's crystallography, physical and chemical properties, names and varieties, occurrence, use and diagnostic features. The description of quartz, for example, takes up two pages, with a long section on names and varieties and a good diagram of its crystal structure: there are then five pages of superb photographs of quartz and its varieties. This is a beautiful book and, at £17.99, should be on the bookshelf of anyone interested in minerals.

Elizabeth Maddocks, BA (Open)

The Little Book of Planet Earth by Rolf Meissner, 2002, Copernicus Books (Springer-Verlag New York), 202 pp. £16 (hardback) ISBN 0387952586.

Copernicus Books are one of America's leading publishers of popular science, and they have quite a shelf of most attractively produced "Little Books of..." - time, bees, stars, the big bang, and now planet earth, originally published in German. The author, a geophysicist and meteorologist, appears to have englished his book himself, and all through there are little infelicitous expressions. Don't let that put you off, though - this would make a good Christmas present for those godchildren, nephews and nieces, or friends whom you've always wanted to introduce to earth sciences. It's nearly always clear and well laid out. Perhaps oddly for a meteorologist, he does not say enough about oceanography, and in the chapter on the Phanerozoic a quick gallop down the eras produces a rather bumpy ride. Various continental configurations and various bits of the story of the development of organisms appear, rather at random. Did you know that trilobites were "forerunners of crayfish"? And (writing immediately after the symposium) I notice that there is no mention of insects.... "Snowball Earth" is treated as an undoubted fact. It is strange to find Milankovitch cycles, a key feature of Planet Earth, only mentioned near the end, in the chapter on "Biological Evolution", and under the sub-heading "Human Evolution and Climate"! Not for your own shelves - you know it all! But a present, yes.

Philip Clark, BSc (Hons), MA (Oxon)

Assynt and Coigach Area by Tim Lawson, 2002, Geographical Association and British Geomorphological Group, 51pp, £8.95 (paperback) ISBN 1843770172.

Published in the series 'Classic Landform Guides' this booklet is a welcome edition to the previous twenty or so that have preceded it. Comprising fifty pages, it covers the North-West area of Scotland from Point of Stoer, Eddrachilis Bay and Loch a' Chairn Bhain in the north, to Ben Mor Coigach in the south, from Ennard Bay in the west to the Assynt mountains in the east.

The main aim of the book is to study the geomorphology of the area and the processes that create and modify the landforms. Beginning with a four page introduction, a brief overview of the hard rock geology is given and deals with the major rock types, structures and geological history. The rest of the book is devoted to seven classic localities and the effects that glaciation has had on the varying rock types resulting in the topography that we see today. These localities are, Stac Pollaidh, Canisp and Stronchrubie, Lochan Tuath, Beinn an Fhurain, Traligill Valley, The Alt nan Uamh Valley and the Stoer Peninsula. A glossary and bibliography completes the work. The text covering each locality is clear, concise and interesting, ample use has been made of photographs, maps and diagrams the quality of which is excellent, these, together with map references, notes on accessibility both by car and on foot make this an admirable field guide that can only enhance our knowledge of this area.

Alan Diggles OU Tutor